AN EVOLUTIONARY MICROCOSM: PLEISTOCENE AND RECENT HISTORY OF THE LAND SNAIL P. (*POECILOZONITES*) IN BERMUDA

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ABSTRACT

Poecilozonites, an endemic element of the Bermudian waif biota, is a remarkable genus of pulmonate land snails that has undergone an adaptive radiation comparable in scope with the classic insular speciation and ecologic differentiation of Darwin's finches. This study considers all Pleistocene and Recent taxa of the subgenus *P.* (*Poecilozonites*) and represents an attempt to treat evolutionary problems with the techniques of multivariate biometry.

The ontogeny of *Poecilozonites* is characterized by complex allometric trends generated by the interplay of protoconch dimensions and post-natal growth gradients. Comparisons among samples must be based upon non-redundant variables considered at a uniform shell size; techniques are presented for reducing raw data to meet these specifications.

An alternating sequence of glacial red soils and interglacial carbonates forms the geologic column of Pleistocene Bermuda. Red soils represent weathering at times of low sea level when modern Bermuda was at the interior of a land mass ten times its present size. Marine and eolian carbonates reflect the high sea levels of interglacial periods.

The polytypic species *P. cupula* includes three former "species"—*P. cupula cupula* (Gulick), *P. cupula dalli* (Gulick), and *P. cupula cupuloides* (Peile)—and two new forms—*P. cupula triangularis* and *P. cupula multispira*. These taxa conform to modern requirements for subspecies: each is morphologically distinct, continuously distributed in time, and uniquely located in a segment of the species range shared by no other conspecific form. Four subspecies exhibit a four-state color polymorphism; the fifth, *P. cupula cupula*, probably evolved from a local population of *P. cupula cupuloides* that had stabilized the most intensely colored morph. This supposition is supported by the pervasive positive correlation between size and color intensity; *P. c. cupula* is largest among the subspecies, while shells of the strongly colored morph exceed others in size both within and among local populations of *P. c. cupuloides*. The species became extinct about 120,000 years ago when Bermuda was nearly inundated by a eustatic rise that exceeded the present sea level by 20 meters.

The typological compendium of shapes that formed the previous classification of giant *P. nelsoni* is superseded by an arrangement based on criteria of the biological species concept. The geographic distribution of morphological variation within red-soil samples indicates that all belong to a single subspecies, *P. nelsoni nelsoni* (Bland). The smaller thick-shelled eolianite form, *P. nelsoni callosus* Gulick, is found in strata sandwiched between the two red soils in which *P. n. nelsoni* occurs. The literal interpretation of chronological subspecies in zig-zag evolution is not accepted; the two taxa are geographic subspecies, migrating with their preferred environments. A closely allied species, *P. superior* sp. nov., lived sympatrically with *P. nelsoni;* it too developed red-soil (*P. s. superior* subsp. nov.) and eolianite (*P. s. arenicolus* subsp. nov.) forms. The eolianite taxa of both species display a set of features adapted to warm interglacial climates and high calcium content of the carbonate dunes.

During the last 300,000 years, the conservative, central stock of *P. bermudensis* (*P. b. zonatus* Verrill) has given rise, in iterative fashion, to four similar, paedomorphic offshoots: *P. b. fasolti, P. b. sieglindae, P. b. seigmundi* (all new), and *P. b. bermudensis* (Pfeiffer). At adult sizes, each is, in comparison with the central stock, more weakly colored, thinner shelled, relatively wider, and more weakly domed; these are the outstanding juvenile features of *P. b. zonatus*. The paedomorphs are distinct genetic entities, not environmentally produced variants: they arise at the periphery of ancestral geographic ranges and lose genes that characterize adult stages of their non-paedomorphic progenitors. The adaptive significance of paedomorphosis may be related to the advantages of thin shells in the low calcium environment of red soils. No paedomorphs evolved in dune environments while the most intensely paedomorphic species developed in red soils.

In addition to branching, *P. bermudensis zonatus* itself displays fluctuating trends in morphology that correspond to ice-age climatic oscillations. Shells are thinner and smaller at a given whorl number in red soils, thicker and larger in eolianites. Modern land snails, exposed to a climatic

range similar to that of the Bermudian Pleistocene, exhibit the same trends in shell form. Again, the thin shells of red soils reflect an environmental deficiency of calcium for shell construction.

P. bermudensis and *P. cupula*, although widely overlapping in range, occupied different ecological realms and did not ordinarily inhabit the same locale. The two known instances of contact produced interspecific hybrids.

PREFACE

My first meeting with *Poecilozonites* was an accident. While rummaging through the fossil collection of Antioch College in 1962, I was attracted to a 1944 newspaper headline—"Red Army Drives for Warsaw"—and found the R. W. Sayles collection of Bermudian snails underneath. I resolved to study this remarkably diversified endemic genus and, after the usual scaling down of initial plans, produced a Ph.D. dissertation on the species *P. cupula* and *P. bermudensis* in 1967. To this, I have now added studies of *P. nelsoni* and *P. superior,* thus completing the subgenus *P.* (*Poecilozonites*). I have collected snails from all known Bermudian localities and have seen the museum collections of all previous workers.

Quantitative techniques were indispensable in deciphering the evolutionary history of this subgenus. I used 44 variables to characterize 1560 specimens and examined thousands more. The techniques, though suitable for numerical taxonomy, are used here for another purpose—to extract evolutionary data from shells belonging to well-established taxa.

Five evolutionary essays (Chapters 5–10) form the heart of this work. I have tried to structure each essay about a major issue in the evolutionary biology of pulmonates (the nomenclature and cause of exuberant morphological diversity in Chapter 6, the biospecies in paleontology in Chapter 7, the relationship of form and environment in Chapter 9). I hope that readers lacking time for the entire work will concentrate on these essays. In this expectation, I have tried to give them a dual status—as part of a unified whole and as independent entities. To enhance the second role, I have eliminated terminology depending on earlier chapters (computer code names for variables, for example) and have minimized the necessary preliminary reading (only Chapters 2A, 4, and 5A need be skimmed first).

It is easy, after a work is completed, to see its shortcomings. My quantitative comparisons among samples, for example, are based only upon differences among means. While variances were used to test the statistical significance of mean differences for all major conclusions, this use of variance as a tool does not exploit its full potentiality, for differences in variation may be as important as differences in means. It is only our residual typological bias that directs us to the latter path. In 1903, Gulick noted, quite correctly, that a major difference between *P. nelsoni callosus* and *P. nelsoni nelsoni* lay in the lowered variability of spire height in the former.

I am especially indebted to my teachers and advisors at Columbia University: R. L. Batten, J. Imbrie, N. D. Newell, B. Schaeffer. T. R. Waller adapted his program DASAN for my use; had I known the magnitude of required effort, I would not have dared to make the request. R. Turner kindly aided me in dissections. W. S. Broecker and D. Thurber supplied radiochemical dates. The curators of several museums have provided both hospitality and specimens: R. T. Abbott and R. Robertson of the Philadelphia Academy of Natural Sciences, J. F. White of Antioch College, L. Mowbray and F. Higgenbottom of the Bermuda Museum, W. Clench of the Museum of Comparative Zoology, C. MacClintock of Yale University, N. D. Newell and R. L. Batten of the American Museum of Natural History. W. Sutcliffe, director of the Bermuda Biological Station, opened the facilities of that institution to me. This work is Contribution No. 466 of the Bermuda Biological Station, supported, in part, by N.S.F. grant GA901. F. T. Mackenzie and L. Land spent three summers puzzling over problems of Bermudian geology with me. I was aided in field collecting by F. T. Mackenzie, L. Land, G. Greiner, G. Brunskill, M. Hamilton, and a host of Bermudian children who curiously watched and sometimes aided while a stranger hammered at their roadcuts. I particularly thank the anonymous four-year-old who found the type specimen of *P. cupula multispira.* K. E. Chave, R. Schmalz, H. B. Rollins, and N. Eldredge have contributed valuable suggestions. M. Rosenberg, R. Houston, C. Jones, and S. Brocoum compensated for my artistic inadequacies by preparing the figures. I thank R. Adlington for photography and E. Gould and A. Pilot for typing various drafts of the manuscript. The traditional *mea culpa* for remaining errors applies, of course.

I. INTRODUCTION

A) Time in Paleontology

Paleontologists like myself who were attracted to their profession by the excitement of evolutionary theory are often chided by other evolutionists for entering an "unproductive" area of the field. The difficulty of drawing sound conclusions from material so inherently limited is often discouraging, so much so that were it not for one unique attribute, I doubt that many evolutionists would seriously consider the study of paleontology. That attribute is, of course, time. I doubt that principles derived from studies of living populations carried out in the course of a man's lifetime can provide a completely satisfactory model for processes occurring during the millennia that elapse in the history of nearly every significant phylogenetic event. At the least, paleontologists must be consulted to assess the consistency of principles derived from studies of living animals with the events of life's history; at best, direct consideration of the fourth dimension will provide new themes. An incorporation of insights gained from the study of vast time spans might increase the generality of evolutionary theory in much the same way that a consideration of high velocities modified Newtonian physics.

If time, in the sense of duration, is the desired quantity, then chronological placement of this segment assumes no great importance—1/2 million years of the Pliocene seems as desirable as an equal slice of the Cambrian. Given the inherent difficulties of paleontological studies, a time slice as close as possible to the present presents many strong advantages; preservation of fossils is apt to be good and closely related living populations provide a rich source for genetic and ecologic inferences.

B) An Evolutionary Microcosm

I have chosen a small time slice, a period bounded by the present and extending back into the Pleistocene no further than 500,000 years. Furthermore, this study is restricted to a subgenus of land snails endemic to the Bermuda Islands, now 19¼ square miles in area. Thus, the title of this work—An Evolutionary Microcosm. That such severe substantive limitation is often required for the abstraction of general conclusions seems ironic, but explanation of a phylogenetic event—the subsumption of its antecedent conditions under general laws of evolutionary theory—requires the reduction of those conditions to manageable proportions by the elimination of confusing variables. And it is from series of such explanations that general conclusions can be formulated concerning the operation of evolutionary processes in the history of life.

In this study, the major advantages of a twofold substantive limitation are as follows:

1. Of a small time slice including the present:

a) Fine stratigraphic control can be attained in Bermuda, where 10 formations (7 bearing abundant specimens of *Poecilozonites*) span no more than 1/2 million years. Very close approaches to contemporaneity in correlations are possible.

b) With the time separating samples in vertical sequences measured in years rather than millennia, the possibility of finding successional populations in true genetic continuity is greatly enhanced. Most phylogenies established from fossil data, on the other hand, are reasonable morphologic series whose major virtue compared with phylogenies derived from modern forms is not that true ancestors are discovered but rather that the inferred phylogeny is not inconsistent with temporal requirements for the actual sequence.

c) Specimens are widespread, abundant, easy to prepare, and excellently preserved. Preservation of coloration patterns, sufficiently rare in Paleozoic and Mesozoic fossils to warrant special notice (e.g., Foerste, 1930; Hayasaka, 1953; Stokes and Stifel, 1964), approaches 100 per cent in these snails. The invaluable nature of color markings in infraspecific studies of land snails is evident in all the major works of this century—the studies of *Cepaea* (reviewed in Harvey, 1964), *Partula* (Crampton, 1916, 1925, 1932), *Achatinella* (Gulick, 1905; Welch, 1938, 1942, 1958), and *Liguus* (Pilsbry, 1912). Pleistocene color patterns in land snails have been briefly considered by Diver (1929) and Owen (1963, 1965, 1966). Absence of the protoconch, a handicap requiring the use of dubious approximations in the estimate of whorl numbers (e.g., Young, 1952, and Sadlick and Nielson, 1963), is a great hindrance to the biometric study of Paleozoic snails. The importance both of protoconch variables themselves and of the precision gained in unambiguous specification of whorl number is evident in the recent monograph of Fischer, Rodda, and Dietrich (1964). Discernible protoconchs remain in more than 95 per cent of the Bermudian specimens.

d) One of the three species of *P.* (*Poecilozonites*) has living representatives. *P. bermudensis bermudensis* is easily reared and bred in the laboratory.

2. Of a small and isolated geographic area:

a) The effects of migration in the confounding of phyletic inferences is virtually removed. With the exception of some Pacific islands, Bermuda is as isolated a spot of land as anywhere on the globe; *Poecilozonites* is a highly distinct endemic genus whose ancestors reached Bermuda long before deposition of the preserved Pleistocene sequence. Migration is no minor problem. The two most famous invertebrate fossil phylogenies, those of the echinoid *Micraster* and the bivalve *Gryphaea*, have recently come under attack with claims that an inferred *in situ* evolutionary sequence is better interpreted as a migration of the "derived" form from another area. Thus, Nichols (1959) believes that *Micraster senonensis* invaded the range of *M. cortestudinarium* but did not split off from it; and Hallam (1962) attributes to migration from elsewhere the first appearance of *Gryphaea* in the Lias of Britain.

The elimination of confusing variables in island situations has been stressed by Miller (1966: 16): "We can see the events of extinction, supplanting and mixture which are so complex on continents as usually to defy interpretation. Island situations are akin to simple lab tests, and from them principles may be determined that are applicable to the whole evolutionary process that moves forward on the continents or in the ocean basins."

b) With a very few square miles to explore and abundant specimens widely distributed, collections cover a large percentage of the total inhabitable area. Hecht (1965: 309) remarked that "If the basic principle of allopatric speciation is true, then the particular difficulties of paleontological research can make it nearly impossible to demonstrate the origin of species by known processes of speciation." In certain cases, however, temporal and geographic resolution in Bermuda is sufficient to demonstrate that phyletic splitting occurred at the periphery of species ranges.

C) Previous Studies of Pleistocene Pulmonates and Prospectus for this Work

Extensive and excellent studies of Pleistocene pulmonates have been undertaken by paleontologists who find in their distribution patterns a record of ice age climatic fluctuations. Although extinction is frequently observed, a surprising result of these studies is the extreme paucity of evidence for the origin of any new taxa, either by speciation or phyletic evolution, during the Pleistocene. According to F. C. Baker (1937: 72), "the majority of the species lived throughout the entire Pleistocene epoch with but little change." Franzen and Leonard (1947: 394) found that "the pupillids of Kansas and of the adjoining areas included in this study do not present a study of evolutionary progression." D. W. Taylor, in his monograph on western North American forms, could cite but one doubtful case of origination, the derivation of *Gastrocopta cristata* and *G. procera* from *G. franzenae* on the dubious criterion that the ancestor's "range of variation includes specimens similar to both of the recent species" (1960: 93). Taylor believes, however, that this split may have been pre-Pleistocene. Hibbard and Taylor (1960), studying (1960: 5) the "most nearly complete latest Cenozoic faunal succession that is known for a small area anywhere in the world," discovered only one tentative origin. the derivation of *Promenetus exacuous exacuous* from *P. exacuous kansasensis* during the late Pleistocene. Commenting further on this case, Taylor (1965: 605) notes that "this interpretation is entirely speculative; if valid, it would be the only exception to the statement that the effects of the Pleistocene have been entirely destructive, not creative, at the specific level." And further, (1965: 602) "The span of Pleistocene times has been brief compared to the duration of molluscan species as identified by shells." Lozek, the major European student of Pleistocene pulmonates, finds that extinction of some forms is the only stratigraphic (i.e., evolutionary) significance of these mollusks (1965).

I find this surprising, because modern studies would indicate that pulmonate land snails, with their small populations, sedentary habits, and rapid adaptive response to selective pressures of environment and predators, are unexcelled among metazoa as material for evolutionary investigation. Welch (1942), for example, described 75 subspecies and 60 geographic races of the Hawaiian tree snail *Achatinella apexfulva;* and though we may question the categorical ranking of his taxa, the diversity is real and cannot possibly represent a situation *in statu quo* since the Pliocene. We must therefore ask whether the discrepancy between Pleistocene and Recent studies is real or is an artifact of limitations in evidence or approach. A few arguments for real distinction may be advanced—most Pleistocene studies are of rather homogeneous continental areas, while many of the best-known modern forms inhabit island chains and have diversified in a manner characteristic of such habitats—but I believe that the following reasons strongly suggest that the observed differences are artificial:

1. A question of semantics: The criterion employed by paleontologists for recognition of evolutionary origin is specific or at least subspecific difference (variously defined) in shell morphology. Paleontologists have generally not looked for the patterns of infraspecific diversity that provide most of our evolutionary data on Recent land snails.

2. Definitions color thought: Given this criterion and the null result of its application, the paleontologist is encouraged to regard the Pleistocene land snail species as a static indicator of a specified environment.

3. A question of interests: Pleistocene climate and stratigraphy, rather than evolu-

tion, is the focus of interest brought to most of the paleontological studies.

4. Interests designate methodology: The quantitative methods required to discern patterns of infraspecific variation are not used by paleontologists, who employ an abundance approach to map the geographic distribution of static entities.

5. Material limitations: Much of the Pleistocene fossil material is not well suited to evolutionary study. Genetically significant infraspecific variation has been most often noted in patterns of coloration, not in the linear dimensions and ratios of gross morphology. If color is not preserved, many well-differentiated geographic isolates meriting taxonomic distinction under precepts of the biological species concept may be unrecognizable.

I do not want this list to be read as a criticism of previous paleontological endeavor. I merely point out that Pleistocene land snails have not yet been approached by paleontologists whose interests and methods are directed towards the gathering of data on the operation of evolutionary processes in time.

This study, then, is a probe in these evolutionary directions; it represents an attempt to deal with four questions which epitomize the types of description and explanation most relevant to such work:

1. Can coherent patterns of morphologic variation in space and time be defined [here quantitatively]?
2. Can an evolutionary history be inferred from these patterns?
3. Can the operation of definite evolutionary processes be identified as productive of this history? In other words, can the efficient cause of observed evolutionary changes be specified?
4. Can the adaptive advantage of modified morphologies be ascertained? [Here, in particular, is there a simple relation between such changes and climatic fluctuations of the Bermudian Pleistocene?] In other words, can the final cause of observed evolutionary changes be inferred?

II. BACKGROUND TO THIS STUDY

A) The Geology of Bermuda

> Malocological problems must be solved within the framework of geology.
>
> Lozek, 1965: 205

Since the geological work of Land, Mackenzie, and myself has appeared elsewhere (Land, Mackenzie, and Gould, 1967), this section will contain only a general statement, a geologic section and those details required as background to the *Poecilozonites* study.

The Pleistocene sequence of Bermuda is a complex alternating and intertonguing series of marine limestones (shallow water and intertidal), wind-deposited carbonate dunes (eolianites), and red soils. *Poecilozonites* is found in the eolianites and red soils, being particularly abundant in unindurated zones of the eolianites (areas vegetated during pauses in dune accumulation). Few snails lived in the inhospitable dunes and few shells survived the solutional weathering which occurred after burial in red soils.

The challenge of Bermudian geology is to interpret these environments of deposition in terms of a synthesizing concept or independent variable—the rise and fall of the Pleistocene sea.

Sayles's (1931) idea that glacially-determined eustatic movements could account for the sequence of strata on Bermuda established a theme which, in Bretz's words (1960: 1753), " . . . probably will never be superseded." Eolianites and soils, which had not been given separate formational status by previous workers, became, for Sayles, the markers of glacial and interglacial times. He correlated times of eolianite formation with glacial episodes, suggesting that lowered sea level exposed a source of sand which, blown by strong winds and unimpeded by vegetation, migrated as desert dunes to form the present islands. Rising interglacial seas cut off the source of supply, and such periods were recorded by extensive soil formation.

TABLE 1. STRATIGRAPHIC COLUMN OF BERMUDA

Formation	Description	Interpretation
Recent	poorly developed brownish soil or crust	interglacial
Southampton	complex of eolianites and discontinuous unindurated zones	
St. George's	red paleosol of island wide extent	glacial
Spencer's Point	intertidal marine, beach and dune facies	interglacial
Pembroke	extensive eolianites and discontinuous unindurated zones	
Harrington	fairly continuous unindurated layer with shallow water marine and beach facies	
Devonshire	intertidal marine and poorly developed dune facies	
Shore Hills	well-developed red paleosol of island wide extent	glacial
Belmont	complex shallow water marine, beach and dune facies	interglacial
soil (?)	a reddened surface rarely seen in the Walsingham district	?glacial?
Walsingham	highly altered eolianites	interglacial

Sayles's stratigraphic column is the basis for that adopted here.

Bretz (1960) accepted the eustatic control of soil-eolianite alterations, but completely reversed Sayles's scheme. He proposed that " . . . the Bermuda dunes are coastal deposits, tied closely to their source of sand, the beach. Their fixation was prompt because of incipient cementation. They did not wander inland" (p. 1747). The substitution by Bretz of rapidly-cemented coastal dunes for Sayles's migrating desert dunes leads to a correlation of eolianite deposition with the high sea stands of interglacial periods. During glacial times, when the sea stood a few hundred feet below the present platform, soils formed over the area of modern Bermuda.

The stratigraphic column of Bermuda is presented as Table 1. The following notations summarize the Pleistocene history of Bermuda in the context of these formational names.

Walsingham: The Walsingham Formation, a complex of eolianites, underlies Belmont marine limestone in many areas of the Walsingham district (best seen at locality 5—Government Quarry—see Fig. 1 for a map of Bermuda). A reddish soil of unknown significance makes up part of the Walsingham complex at localities 5 and 9. The soil seems too persistent and strongly developed to represent a mere pause in dune accumulation, yet it lacks the depth of weathering and strong solutional features associated with red soils formed during glacial periods. Walsingham rocks underwent diagenesis prior to Belmont deposition (highly altered Walsingham clasts in uncemented Belmont conglomerate at locality 5). Thus, a glacial episode may separate the Walsingham and Belmont formations.

Belmont: The Belmont Formation is represented in most areas of its outcrop by marine limestones standing slightly above present sea level. At one time, however, the Belmont sea rose to +23 meters (marine conglomerate deposited against a sea cliff cut in Walsingham eolianite exposed at locality 5). Eolianites of Belmont age underlie and overlie the marine limestones in several places.

Shore Hills: The Shore Hills is the best developed red soil of Bermuda, reaching thicknesses of 12 feet in deep cylindrical solution pipes (popularly known as "palmetto stumps"). Snail shells are not abundant in the red, deeply weathered portions of the soil, having been destroyed by solution, but are fairly common in fissure fills of this age. All of Bermuda's extensive caves were cut during Shore Hills time, when percolating fresh water attacked the underlying carbonates.

Devonshire: The sea rose again to an elevation of +5 meters (wave cut notch at Hungry Bay, locality 49). The Devonshire Formation consists of intertidal sandy and conglomeratic deposits formed during this transgression. It is frequently found in erosional unconformity atop Belmont marine limestone, the Shore Hills soil having been stripped off. Radiochemical dates have been obtained from Devonshire corals (localities 2 and 51); each of four specimens indicates an approximate age of 120,000 years (W. S. Broecker, personal communication).

Harrington: The Harrington Formation, a poorly indurated calcarenite ("accretionary soil" of previous authors), formed as the Devonshire sea retreated. That it records a falling sea is indicated by the common vertical gradation from white sands with marine fossils at its base to brownish [carbon stained from terrestrial vegetation (?)] sands with abundant land snails at its top.

Pembroke: As the Devonshire sea continued to fall, carbonate detritus became available for deposition as Pembroke eolianite. Dune building was not continuous, since unindurated zones, representing pauses in dune accumulation, are common in this formation.

Spencer's Point: The sea rose again, certainly to +11 meters (east of locality 32) and possibly to +20 meters at Black Watch Pass (locality 6), depositing patchy intertidal conglomerates along the south shore and extensive marine and eolianite units on the north shore. A Spencer's Point coral obtained from a displaced block on Saucos Hill (locality 41) yielded a radiochemical date indistinguishable from those of Devonshire corals. This produces a stratigraphic puzzle to which three potential solutions may be offered:

1. The displaced block is Devonshire float. This can almost surely be discounted, since the block, weighing several tons, lies 10 feet downhill from Spencer's Point material of similar lithology. The nearest Devonshire is 1/2 mile to the west at Devonshire Bay.

2. There is only one post-Belmont marine limestone. The extensive unindurated zone lying below this coral and previously correlated with Harrington overlying Devonshire at Devonshire Bay belongs to a Belmont eolianite complex. Instead of one unindurated zone and two limestones, we have one limestone and two unindurated zones. This explanation seemed most probable until Mackenzie and Land found evidence of two limestones in superposition at Spencer's Point itself (locality 35).

3. Deposition of the entire Devonshire-Spencer's Point suite was so rapid that the 10–15 thousand-year uncertainty of the thorium dates does not allow a distinction of the limestones; the limestones would then represent two phases of a 120,000-year sea, evidence of which is now being uncovered in many areas (Broecker, 1966). Could the extensive Pembroke eolianites be deposited in so short an interval? Observations of the rapid growth of dunes active on Bermuda during the 19th century affirm this possibility. Thomson described the dune movements in his *Challenger* volume (1877: 310–311):

> There is a wonderful 'sand glacier' at Elbow Bay . . . The sand has entirely filled up a valley and is steadily progressing inland in a mass about five-and-twenty feet thick . . . [One resident] was either too late in adopting precautionary measures, or perhaps submitted hopelessly to his fate, for all that now remains of his cottage is the top of one of the chimneys projecting above the white sand like a tombstone.

St. George's: Although the St. George's soil is not as well developed as the underlying Shore Hills, it too records a period of diagenesis during lowered sea levels of a glacial period.

Southampton: As the sea rose, a new period of dune building commenced. The Southampton Formation, a complex of eolianites and unindurated zones, reaches thicknesses of greater than 200 feet in southwest Bermuda. Much of southwest Bermuda is entirely Southampton in age; the main island has been accreting in that direction, the major source of Bermuda's winds (Mackenzie, 1964). No marine Southampton has ever been found (marine Pembroke is likewise unknown), and Southampton seas must have stood below the present level. (No evidence for Pleistocene tectonism has been uncovered on Bermuda, and the islands may represent a good "tide gauge" for the assessment of Pleistocene eustasy.)

Recent: Dunes active during the 19th century have become stabilized by vegetation. A brownish soil derived from weathered eolianite underlies many vegetated areas; bare stretches are covered by a solutional crust. Much modern topography reflects the depositional profile of Southampton dunes. Red soil is present in lowlands, which were never covered by Southampton dunes.

B) Natural History of Poecilozonites in Bermuda

The native Bermudian biota is a classic instance of the depauperate and disharmonious associations characteristic of isolated oceanic islands populated by chance dispersal from distant continental areas. Birds excepted, a small lizard of the genus *Eumeces* is the only native tetrapod (even the inevitable rat required human transport). Only one other large pulmonate — *Succinea* — is found as a fossil. Verrill's treatise (1901–1902) remains the major work on the Bermudian biota and its origin.

Of *Poecilozonites* itself, Pilsbry (1900: 494) had the following to say: "The endemic element (*Poecilozonites*) undoubtedly long antedated the other forms, as its generic divergence and strong specific differentiation indicate. In all probability it was derived from the Eastern United States by some rarely efficient means of transport." A member of the Zonitidae, *Poecilozonites* most closely resembles North American species of *Gastrodonta* and *Ventridens* in its genitalia, but is extraordinary in lacking the pedal furrow supposedly characteristic of aulacopod pulmonates. Pilsbry (1924) assigns it subfamily rank.

In his dissection of the genitalia, Pilsbry (1889) found a cleft spermatheca, one branch of which originated at the base of the penis. He wrote (1889: 85): "The connection of the duct of the spermatheca with the penis is unique as far as I know, in the Pulmonata, and suggests the probability of self-impregnation." With the kind assistance of Dr. Ruth Turner, I have been able to verify this observation. The occurrence is not, however, unique. According to Taylor (1900: 371), the cleft spermatheca with penile branch is found in "the North American Gastrodontae," the supposed ancestors of *Poecilozonites*. Pilsbry's designation of the Gastrodontinae as ancestral, established primarily on shell form, is thus affirmed. Moreover, the capacity for self-impregnation may help to explain the success of *Poecilozonites* in establishing itself on Bermuda. More than the sheer accident of first arrival may be involved, since the chance introduction of any single individual is so much greater than that of a pair or pregnant snail.[1]

Its time of arrival is unknown and cannot be inferred by extrapolating rates of the last 300,000 years; for early in its history, *Poecilozonites* underwent a vigorous and presumably rapid adaptive radiation. When *Poecilozonites* is encountered in the oldest Bermudian formations, it is strikingly diversified into three subgenera and 15 species (Peile, 1926). These range in size from giant *P. nelsoni* (maximum diameter 46 mm) to small species of the subgenera *P.* (*Gastrelasmus*) and *P.* (*Discozonites*), which rarely exceed 5 mm in diameter. In their morphologic variety, the species of *Poecilozonites* provide an excellent parallel to such famous cases of insular diversity as Darwin's finches and the Hawaiian honeycreepers. I assume, continuing the parallel, that the various species of *Poecilozonites* filled a spectrum of ecologic roles occupied by several genera in continental areas. The ecologic and geographic situation of Bermuda provided just those conditions outlined by Carlquist (1966) as evocative of rapid evolution on islands: lack of competitors and predators, a broad range of ecologic opportunity, and numerous potential geographic barriers.[2]

The native biota of Bermuda has fared poorly under the onslaught of species introduced by man. The indigenous flora was ravaged by hogs late in the 16th century and by rats early in the 17th; the famous Bermuda "cedar," *Juniperus bermudiana*, was nearly destroyed in this century by a scale blight. The vulnerability of island biotas to introduced competitors is well known (Simpson, 1953: 296; Mayr, 1963: 74). Carlquist (1966: 21) writes of the Hawaiian flora: "Almost any introduced continental species of plant seems capable of replacing autochthonous species of comparable ecological requirements."

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[1] In particular, the arrival of a very small immature snail might be sufficient to establish the species. The abundance of microgastropods in the Bermuda Pleistocene indicates that small forms have a vastly better chance of introduction. *Poecilozonites*, of course, does not normally reproduce by self-fertilization. I have often observed their elaborate copulation ritual. I shall soon be conducting experiments to determine whether a *P. bermudensis bermudensis*, isolated from the time of hatching, will impregnate itself.

[2] I have undertaken some rather casual experiments which indicate that the modern reptiles and amphibians of Bermuda, including the native *Eumeces*, would rather starve than eat a *Poecilozonites*. Birds constitute the most likely source of predation, though there is no evidence, either direct or indirect ("anvils," etc.) of such. Bermuda now consists of 6 major and scores of minor islands.

re 1. Outline map of Bermuda before air force and navy modifications of the shore line. From Sayles (1931). Dotted lines are parish boundaries. Localities are described in Appendix 2.

Of all introduced invertebrates, however, none have proved so troublesome as the pulmonate snails. *Polygyra,* unknown as a fossil in Bermuda, is now the most common land snail on the islands. In the late 1880's, the "spiral snail" *Ruminea decollata,* introduced by Governor Lefroy in 1876, was inflicting so much agricultural damage that the Bermudian Government sponsored a prize contest for the development of "efficaceous, expeditious and economical methods to effect its extermination." (Bermuda Historical Society Documents, Hamilton, Bermuda). Pilsbry (1900) expressed surprise that *Otala lactea* had not managed to intrude itself, but his statement was negatively prophetic in the light of a recent *Otala* invasion. Despite the local legend attributing its introduction to a wartime visit of General De Gaulle, the arrival of *Otala* dates from 1928 when snails "brought into the colony to be tried as a food . . . subsequently escaped from captivity" (Bennett and Hughes, 1959: 432). Dr. Hughes tells me that the specimens came from New York's Fulton Fish Market and won their liberty by crawling out of a paper bag left on the offender's porch. The speed of their spread was colossal. *Otala* is now omnipresent on Bermuda, though its numbers have been substantially reduced by the "cannibal snail" *Euglandina rosea,* introduced from Hawaii as a biological control in 1958 (Simmonds and Hughes, 1963).

The effect on *Poecilozonites* of human introductions and disruptions of the native biota has been profound. Although two species, *P. bermudensis* and *P. circumfirmatus* are still common in many areas, they are absent over a wide range of potential habitat and constitute a small fraction of the total pulmonate fauna.

The reduction from 15 Shore Hills species to a handful of survivors is not wholly the work of man and his agents. Many common Harrington-Pembroke taxa do not appear in the St. George's and later formations, and their extinction can probably be attributed to the intervening high Spencer's Point sea (20 meters above present mean sea level). But other taxa common as fossils in the latest Southampton dunes have never been found alive, and their elimination can probably be traced to man. In addition to competition from introduced snails, *Poecilozonites* species probably fared poorly during the hog and rat plagues which, if we are to believe the early writers, must be ranked in effect with the Australian rabbit invasion. Hogs were introduced, probably by Spanish pirates, in the 16th century and were abundant when the English arrived. The English brought rats, and the plague of 1614–1618 almost destroyed the early settlements. Governor Butler wrote at this time (in Verrill, 1902: 713–714): "They eate up the whole country before them, wheresoever they went, utterly devoureinge all the corne they mett with all in an instant; so that, in despight of all the catts sent from out of England, and the layeinges of poyson, the Governours often fireinges of the whole islands, to the huge waste of much excellent caedar timber, or whatsoever els could be devised against them, they every day more and more so multiplied and grew upon the poore amazed people." All, indeed might have been lost "had not God (who noe doubt hath an especiall worck in the peopling of thes partes with Christians), by his owne hand, in great mercy, swept them all away in an instant." Verrill (1902), taking a less apocalyptic view, attributes their death to starvation. Both hogs and rats will eat snails; rats are often a major pulmonate predator (Liat, 1966). According to Verrill, "probably many species of birds, reptiles, insects, snails, etc. were exterminated . . . by the hogs and rats."

The recent introductions of *Ruminea* and *Otala* have further reduced the numbers and variety of *Poecilozonites.* An elderly employee of the Bermuda Biological Station, a resident of St. David's Island, tells me that in her youth, before the *Otala* invasion, *Poecilozonites* were collected in barrels and burnt. She claims to have seen none in the last decade. The Rev. Lane, winner of the *Rumina* control prize contest, referred to the living *Poecilozonites* as "a degenerated family which has not upheld the stature of its progenitors" (Documents, Bermuda Historical Society). *Sic transit gloria.*

III. GOALS AND METHODS OF QUANTIFICATION

The very term zonitoid connotes an almost featureless shell. H. B. Baker, 1938, p. 6

Of all classes of organisms, the mollusks are perhaps the best adapted for the study of ontogenetic stages . . . since all these stages are preserved as a permanent record in the form of the shell.
Grabau, 1907, p. 609

A) Introduction

The first statement above is a challenge; the second, its partial resolution. A snail shell appears poor indeed when compared with a vertebrate skeleton for enumeration of measurable variables, yet it possesses other features particularly favorable for quantitative evolutionary studies.

1. As an accretionary structure, it retains a complete record of its morphological development. If shape changes during ontogeny, a general occurrence among pulmonates, then a description of the sequence of forms attained at various sizes or whorl numbers provides a basis for interpreting relationships between ontogeny and phylogeny: the size of origin of new features can be determined; phyletic alteration of form can be understood as the cumulative effect of ontogenetic changes in growth rates; paedomorphic or recapitulatory effects can easily be spotted. These possibilities were recognized by some early evolutionary paleontologists, but their approach was often marred by an *a priori* faith in the universality of Haeckelian recapitulation (e.g., Grabau, 1902, 1907).

2. The pulmonate shell is known to be highly expressive of the environmental conditions in which it grows (e.g., Rensch, 1932; Oldham, 1929, 1934). Given this phenotypic plasticity, it will be difficult to distinguish genetic from environmental modification, but selective forces in the environment can often be ascertained and their influence on larger changes with an inferred genetic basis determined.

Measurements have been used in the classic studies of pulmonate diversity (e.g., Crampton, 1916, 1925, 1932), but these have not extended beyond the "standard" dimensions (total length and width, apertural length and width) and derived ratios. Yet these measures of gross morphology have little discriminating power, since similar values are attained independently by population after population. Moreover, when only one set of measures is made per specimen, ontogeny must be inferred from mass curves (Gould, 1966a), thus frustrating the major advantage of studying pulmonate shells in the first place—the possibility of obtaining true longitudinal data, the only kind that can yield information on individual variation in growth (Cock, 1966: 136). Often, to make matters worse, attempts are made to infer ontogeny from curves constructed for a series of adults (among helicids, for example, which have a definite final size varying widely among individuals of a population). Yet, there is no reason why such curves should reflect individual ontogeny in any precise way (Röhrs, 1958, 1959, 1961; Gould, 1966b). This method represents a confusion of two different types of data—longitudinal and static (Cock, 1966).

I have tried to increase the number of variables beyond the conventional set of general size and shape measures in four ways: by the quantification of color variation; by the inclusion of protoconch dimensions; by expanding the set of apertural measures to encompass the many ontogenetic changes in shape not expressed in the width/height form ratio; and by measuring heights and widths at each whorl. The last of these four accomplishes two purposes:

1. A mathematical expression for the geometry of the dome may be derived from the width-height pairs; this expression abstracts the ontogeny of general shape development as a single statement.

2. Since zonitoids continue to grow throughout life and therefore lack terminal growth features defining adult dimensions (such as the expanded and colored lip of many helicids), meaningful size measures must be taken with reference to a whorl number, rather than a (indefinable adult) growth stage.

The resulting set of measures, 33 variables and 11 ratios and combinations, serve to define the form of *Poecilozonites* in sufficient detail to permit a fairly complete reconstruction of the shell from a table of the variables alone. Any important alteration in shell morphology should be capable of identification and definition within the set of measures, and a basis for multivariate comparisons among shells is provided.

Raup, in a series of fascinating papers (1961, 1962, 1965, 1966; see also Thompson, 1942: 748–849), has programmed a computer to generate the forms of coiled shells from four parameters—the shape of the generating curve, the whorl expansion rate, the position of the generating curve with respect to the axis of coiling, and the rate of whorl translation down that axis. Why, then, have more than 30 measures been used in this study?

1. Raup's model produces only the general form of the shell; 7 of my measures deal with color and shell thickness: "It should be emphasized that the four parameters do not completely describe the morphology of the coiled shell. . . . The model is concerned only with general form and includes only that ornamentation produced by the revolution of the generating curve about the axis" (Raup, 1966: 1181).

2. One of Raup's parameters, shape of the generating curve, is composite. In practice, it is drawn rather than defined mathematically when its shape does not approximate a simple geometric figure. To express the shape of a complex aperture in numbers, many variables are needed: I have used seven. "The generating curve is often equivalent to the outline of the growing edge of the shell. As such, its shape can only rarely be defined mathematically. . . . More generally, however, a line drawing is used to describe the shape" (Raup, 1966: 1179).

3. The protoconch (embryonic shell) is rarely constituted in geometric similarity with the rest of the shell as assumed by Raup's model. This introduces a small discrepancy, quite unimportant to Raup's analysis, between the apical regions of actual and computer-generated gastropod shapes. Three variables define protoconch form in this work.

4. Raup's model assumes that geometric similarity is preserved with shell growth. While many marine shells conform adequately to this criterion, significant allometry[1] is almost universal in pulmonates. (The characteristic domed shape, for example, implies that height increases faster than width—Gould, 1966a.) If the allometric trend is regular and gradual, it can often be encompassed within Raup's model by redefining one of the parameters as a variable instead of a constant; gradual decrease of the translation rate produces an "extraconical" shell (Raup, 1966: 1185). Two of my variables relate to the ontogeny of doming in *Poecilozonites*.

5. There is a fair amount of redundancy in my measures, some introduced inadvertently, the rest a by-product of variables needed to construct the derived parameters. Heights and widths at whorls 1 through 5 do not represent 10 independent sources of variation; they are all, however, utilized to define the allometric parameters of shell doming.

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[1] I use the term allometry to describe any size-correlated change of shape, not only those trends in form which can be adequately fitted by power functions (Gould, 1966b: 600–603).

TABLE 2. HYPOTHETICAL DATA MATRICES OF FORM USED IN THIS STUDY

Raw Data Matrices

	Protoconch Width	Width End of Whorl 5	Height End of Whorl 5
Sample 1:			
specimen 1	1.5	25	15
specimen 2	1.6	26	16
specimen 3	1.7	27	17

	Protoconch Width	Width End of Whorl 5	Height End of Whorl 5
Sample 2:			
specimen 1	1.6	26	16
specimen 2	1.7	27	17
specimen 3	1.8	28	18

Matrix of Means

	Protoconch Width	Width End of Whorl 5	Height End of Whorl 5
Sample 1	1.6	26	16
Sample 2	1.7	27	17

6. Our difference of approach reflects a difference of interests. Raup abstracts the general form of coiled shells with as few parameters as possible. Computers can then generate a range of possible forms; this allows us to consider such fundamental questions as: why do actual shells occupy only a part of the range of potential shapes? I am interested in detecting the subtle variations in morphology that characterize geographic variation and incipient differentiation within species.

B) Goals of Quantification in this Study

A data matrix may be treated in two ways: we make comparisons among rows or among columns. [In this study, each column is a variable, each row a specimen (or, in the matrices of means described below, the mean sample values for each variable).] Table 2 presents some simplified, hypothetical data matrices of the form used here.

1. Comparison among rows (specimens or samples): The morphological differences of specimens within and among samples constitute the primary data in any evolutionary study of form. Needham (1950) has suggested the heuristic statement: form = size + shape. Comparisons of "form" may be made on either basis.

a) Size: Size, to be a useful criterion, must be standardized in some way. This is usually achieved by comparing specimens at a definable growth stage, generally the adult. Zonitoids, as mentioned above, continue to grow throughout life. I have therefore been unable to use the maximum size of specimens as a basis for comparison,[1] and a different standard must be sought. Size at a given number of whorls, the usual alternative for zonitoids (Baker, 1938: 5), is used here. A criterion for numbering whorls must then be established, and it is a virtue of the *Poecilozonites* material that "the best and most accurate method" (Sadlick and Nielson, 1963: 1086), counting from the termination of the protoconch, is available. Burma (1948), Young (1952), and Sadlick and Neilson (1963), working with material in which the apical region is rarely found intact, were constrained to use another standard (a "zero point" at which the whorl height equals some arbitrary value). Although the zero point can be determined objectively, it lacks the desirable attribute of making the whorl numbering criterion coincident with a physiologically meaningful point in shell development. When the termination of the protoconch can be used, the zero point is the true beginning of post-hatching growth. Two disclaimers should be made for this method:

i) *Size at a whorl has no* a priori

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[1] This inability is one of the most unfortunate aspects of this work; for maximum size surely varies among samples. The difficulty could be surmounted if the sample sizes were relatively equal and quite large, but too many of my samples are too small even to allow a randomized equalization of sample sizes at a "least common denominator" number.

relationship to the final dimensions attained by the shell. Large size at a given whorl is no guarantee of large final size.

ii) No definite implications of age or "relative age" (Burma, 1948) should be drawn from the whorl number, which serves primarily as a standard for comparison.

b) Shape: Shape is expressed as a dimensionless number (usually a ratio or an angle). The comparison of shape in specimens of different size is the reason usually cited for forming a ratio, but we must avoid the fallacious corollary that the ratio is therefore independent of size. If the relationship of variables forming the ratio is allometric, then the value of the ratio will change as size increases. Thus Franzen (1966) claims that the width/height ratio is useful in separating the succineid pulmonate species *Oxyloma salleana* and *O. retusa.* The ratio varies with size, however, and we are given no assurance that it can discriminate between the two species at a common size. For a single sample of *O. salleana*, mean width/height for specimens > 3 1/2 whorls is 0.654 (observed range, 0.608–0.695, N=4); for specimens < 3 whorls, mean width/height is 0.539 (observed range, 0.510–0.577, N=4).

Almost all bivariate plots of ontogeny in *Poecilozonites* are allometric, and *meaningful comparisons of shape must be made at equal sizes*[1] *or whorl numbers.* It is not easy to decide which of the two affords a better comparison. In *P. cupula*, differences in size-at-a-whorl among the various subspecies is so great that choosing a size of 17 mm, for example, would result in the comparison of a *P. cupula dalli* of 5 whorls with a *P. cupula cupula* of 4 whorls. Since many important alterations of shape occur during growth of the fifth whorl, the choice of 17 mm would occasion the comparison of a *P. cupula dalli* of near maximum (observed) size with a rather juvenile *P. cupula cupula.* Despite the above disclaimer (p. 423), whorl number in *P. cupula* is probably a better criterion of developmental stage than is size. If this is so, then the choice of equal size or equal whorl number as a standard for shape comparisons depends upon whether ontogenetic alteration of form is under the primary control of absolute size or developmental stage. Since definite shape changes tend to occur at similar whorl numbers rather than at a similar size in *P. cupula*, intersample shape comparisons are made at a common whorl number. In *P. bermudensis*, the problem is not so acute, since the size range at a whorl is quite small among samples.

When all variables have been standardized so that their values are recorded at a common size or whorl number, a basis for the meaningful comparison of form among samples is provided in the "matrix of means" (Table 2b), each row of which contains the mean sample value for each of the variables. The mean sample values are obtained in two ways, depending upon the nature of the variable. If the variable is already standardized (e.g., height at the third whorl, whorl number at which the upper color band is formed), a simple mean is calculated. Other measures, particularly the set of apertural variables, are not made at the standardized value, but are taken at the final size of each specimen. (Theoretically, each apertural variable could be measured at, say, the fifth whorl, but this would necessitate the breakage of all larger specimens and the discard of all smaller ones.) In such cases, the predicted value at the chosen common size or whorl number is determined by bivariate regression. The range of measured specimens is

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[1] Size is defined here as width + height. Many ambiguities have been introduced by authors who use height or width alone as the measure of size. Price-Jones (1930), for example, claimed to have demonstrated that large adults of *Cepaea nemoralis* tend to have a high width/height ratio. But since he used total width as his criterion of total size, the positive correlation of "size" with width/height only shows that an adult with an absolutely wide shell tends also to be relatively wide.

selected so that the common size or whorl number is near the midpoint of the measured interval. Only shells of four whorls or more are used to construct the regressions, since a wider size range results in significant departures from linearity. Each variable is plotted against size or whorl number (depending upon the chosen criterion of comparison), and its estimated value at the chosen size or whorl number is determined.

The 810 reduced major axis fits (10 variables in each of 81 samples; 20 specimens per sample)[1] were calculated by DASAN, a FORTRAN 2 program written by Dr. T. R. Waller and kindly modified by him for use in this problem.

2. Comparison among columns (variables): Bivariate regression and correlation are standard methods for comparing variables with one another. When considered over a wide range of size, two variables generally display strong correlation for the trivial reason that most linear dimensions increase as an organism gets larger. Variables may be related for other reasons—similarity of function or mechanical proximity, for example—and it is the aim of correlation studies to provide a body of data from which the causal factors of variable interrelationships can be inferred (see Olson and Miller, 1958). A complete set of such interrelationships can be depicted in a matrix of correlation coefficients. Since the sheer quantity of information in such a matrix is too vast for consideration in raw form (there will be 780 meaningful entries when the interrelationships of 40 variables are assessed), multivariate clustering methods for the abstraction of simpler patterns implicit but difficult to recognize in the raw matrix must be used. Factor analysis, the abstracting method applied here, will be described in Chapter 5.

Differences of form provide the basis for assessing evolutionary relationships among populations. These differences are expressed in terms of variables. We study the interrelationship of variables for two reasons:

a) The recognition of differences in form is purely descriptive. The goal of evolutionary studies is to explain these differences. The study of interrelationships among variables may lead to an identification of causal influences shaping the form of an organism. In a study of pelycosaurian reptiles, for example, I found that widths of limb bones and vertebrae correlated more strongly with one another than with their respective lengths (Gould, 1967). Two major clusters of variables, bone lengths and bone widths, were abstracted from the correlation matrix. Total body length sorted with the bone lengths, estimated weight with the widths. Since terrestrial vertebrates compensate increasing weight by differential thickening of bones responsible for support, the clusters could be explained in mechanical terms. The increased relative thickness of supporting bones in large pelycosaurs is an adaptive response to increased size.

b) Redundancies can be eliminated: The major difficulty plaguing a proper evaluation of the differences in form among samples is failure to account for interrelationships among variables. Two populations are often said to be very distinct because they differ significantly in 20 characters. Built into this statement, however, is the hidden major premise that the 20 characters reflect 20 separate determinants of variation. This premise will usually be false. In extreme cases, the 20 characters will form a tight cluster measuring only one significant dimension of difference. Given the prevalence of allometric trends in ontogeny, phyletic size increase without alteration of ancestral ontogenetic trends will produce an organism differing

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[1] For a few populations, fewer than 20 specimens were available. For samples with abundant specimens (the large majority), all individuals larger than 4 whorls were selected. These specimens were divided into two lots on the basis of size and 10 specimens were randomly chosen from each lot.

from its ancestor in many aspects of shape. The total genetic difference (the ideal basis for assigning taxonomic rank to ancestor and descendant) may be very small or even nil. Corbet (1964) found that the contrast in skull form between island and mainland populations of the bank vole *Clethrionomys glareolus* was a consequence of size differences: "The number of independent characters distinguishing the island races is very small" (1964: 191). Former hypotheses of relict distribution, once deemed necessary from the supposed intensity of genetic divergence implied by differences in skull shape, are not required and the pattern of variation is compatible with a hypothesis of recent accidental introduction from the mainland. In *Poecilozonites*, large relative width and wide umbilicus at a standard whorl number are mechanically correlated. Only one significant dimension of variability is expressed by the two measures.

C) *The Variables and their Measurement*

In this listing, each variable is defined and its method of measurement given in the following format: name of the variable, its computer code name, and a description of the method of measurement if not obvious.

1. Standardized Variables:
  a) Color

1, 2. Whorl number of formation of upper and lower color bands on the upper whorl surface, ONESEUP, ONSELO. Color deposition begins as discontinuous blotches and flames. These variables record the whorl number at which the transition from blotches to a solid band occurs.

3, 4, 5. Percentage of upper whorl surface covered by color bands at the third, fourth and fifth whorl, COLOR3, COLOR4, COLOR5. The width of the upper whorl surface and the width of the color bands on this surface are measured. A ratio is formed: width of color bands/total width of upper whorl surface.

6. Percentage of the lower whorl surface covered by the subperipheral color band at the fifth whorl, LOWCOL. As above, but on lower whorl surface. This measurement cannot be made if the specimen has fewer than 5 or greater than 6 whorls. (In the latter case, the lower whorl surface is covered by the succeeding whorl; the upper whorl surface remains completely exposed in all whorls of *Poecilozonites.*)

  b) Protoconch

7. Width of the protoconch, PRWIDT.

8. Height of the protoconch, PRHIGH. Actually, the height of the protoconch spire; that part of the protoconch below the whorl periphery is covered by succeeding whorls. The protoconch width measure, on the other hand, is the total protoconch width.

9. Number of whorls in protoconch, PRDEGR. Measured in degrees.

  c) Widths and Heights

10, 11, 12, 13, 14. Radius of shell (apex to whorl periphery) at whorls 1 through 5, WIDTH1, WIDTH2, WIDTH3, WIDTH4, WIDTH5. Specimens are mounted in clay on a wooden cube, the axis of coiling perpendicular to the base of the microscope. Width measurements are made from the apex to post-protoconch whorls 1 through 5 along a line drawn from apex to whorl periphery at the end of the fifth whorl and projected to a plane perpendicular to the axis of coiling.

15, 16, 17, 18, 19. Height of spire at whorls 1 through 5, HEIGH1, HEIGH2, HEIGH3, HEIGH4, HEIGH5. After the width measures (10–14) are completed, the wooden block is rotated 90° and corresponding height measures made along the same line, this time projected to a plane parallel to the axis of coiling.

  d) Angles

20. Angle made by top and bottom of fifth whorl with whorl periphery, angle EFG of Figure 2, PSANGL. The specimen is oriented in a box of magnetite granules so that the whorl periphery (line FGC of Fig. 2) is straight, with point F forming

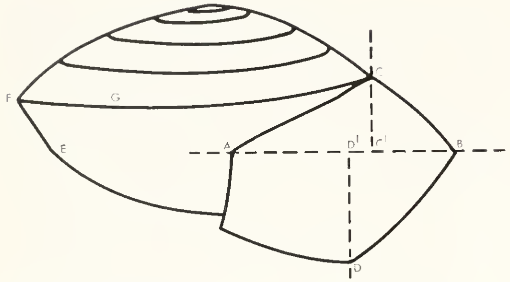

Figure 2. Measurement criteria for apertural variables.

the left extremity of the line segment. The angle is measured by placing the micrometer cross hair in coincidence with line FGC, then rotating it to coincidence with line EF. A protractor is glued to the microscope tube just below the point of contact of eyepiece and tube; a needle is glued to the eyepiece. Rotation of the needle over the protractor gives the angular measurement. I thank Dr. R. L. Batten for teaching me this simple and accurate method.

21. Angle of declination of incremental growth lines at fifth whorl, DANGLE. The specimen is oriented so that a portion of the upper whorl surface at the fifth whorl is as parallel as possible with the base of the microscope. The declination angle is the acute angle made by apertural growth lines with a line drawn tangent to the whorl periphery at the fifth whorl. (Since the incremental striae represent former apertural positions, this method represents a way of standardizing the "aperture inclination," often considered an important variable in describing pulmonate shells.)

2. Measures Derived from Standardized Variables:

22. Ratio of width to height of spire at the end of the fifth whorl, RATIO5. Ratio defined as WIDTH5/HEIGH5, a standardized form ratio.

23. Total size at end of fifth whorl, TSIZE5. Defined as WIDTH5 + HEIGH5. This measure serves as a general size criterion when samples are standardized in a matrix of means.

24. Differential growth ratio, KVALUE. The value of the exponent in the power function (equation of simple allometry)

$$y = bx^k$$

where y is height and x width. When $k > 1$, y is growing faster than x and allometry is said to be positive. Since height increases faster than width in dome-shaped objects, k will always exceed 1 in this study. The higher the value of k, the faster the ratio of raw measures (y/x) rises with increasing size and the stronger the intensity of doming. As will be explained under item 25, however, a high value of k does not necessarily mean that the shell will be relatively high at a standard size near maximum dimensions. That intensity of doming is not a measure of relative height is proven by *Turritella*, rarely excelled in relative height among gastropods, but possessing a triangular cross section and lacking a dome entirely ($k = 1$).

A value of k was calculated for each specimen. The power function provides an accurate approximation of spire geometry from whorl 2 to the end of growth (0.997 is the average correlation coefficient of log y vs. log x). Thus, four points were used in the calculation: (WIDTH2, HEIGH2), (WIDTH3, HEIGH3), (WIDTH4, HEIGH4), and (WIDTH5, HEIGH5).[1] The logarithmic transformation of the power function

$$\log y = \log b + k(\log x)$$

has a linear form in which k is the slope and log b the y intercept. A linear regression program can calculate these parameters when values of the original

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[1] The height of the protoconch was subtracted from each of the height measures. The power function applies only to the accretionary part of shell growth and, on this theme, the width and height variables should be rephrased as "perpendicular distance from axis of coiling at nth whorl" and "total height of accretionary part of shell at nth whorl."

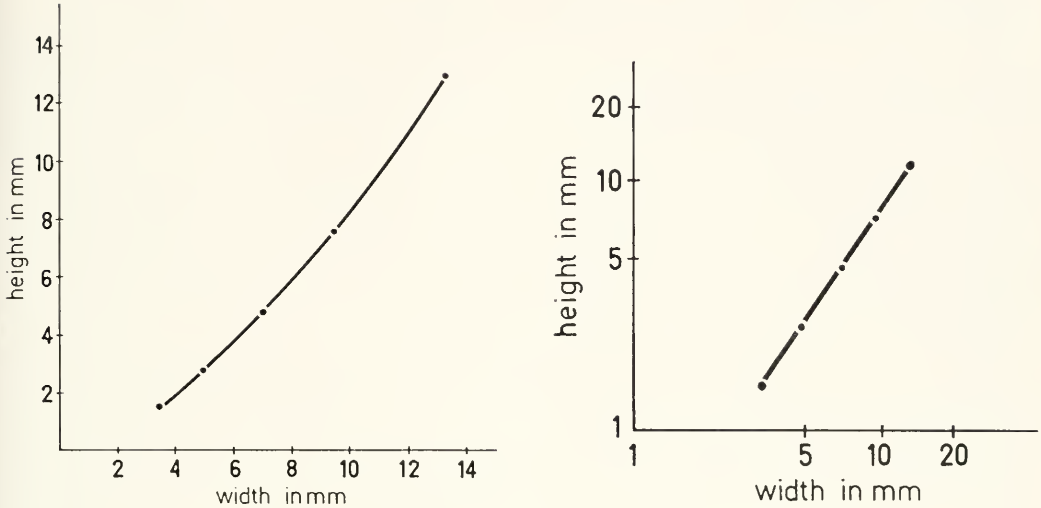

Figure 3. Arithmetic and log-log plotting of width-height pairs for a typical specimen of *P. nelsoni*. 3a (left), arithmetic plot. Curvature represents actual shell geometry as if the cartesian grid were superimposed upon a shell turned upside down so that the apex lies at the origin. 3b (right), logarithmic plot. The straight line indicates that the data are well fit by the power function $y = bx^k$. From Gould (1966a).

data have been transformed to logarithms. k values for more than 1200 snails were computed by DASAN (reduced major axis), and thanks again are due to Dr. T. R. Waller for aid in adapting his program to the peculiarities of this problem. Figure 3 depicts the derivation of this measure in graphical form.

25. Ratio of height to width at the outset of simple allometric growth, INFORM (initial form index). The complete description of a line in a coordinate system requires that two parameters be defined: the slope and the position. The y intercept is usually used as a measure of position. Log b, the y intercept of the log-transformed power function, is an inappropriate measure for two reasons:

a) b is the value of y at x=1. An x value of 1 micrometer unit lies well outside the range of sizes for which the equation is valid (x=30 to 150 units). The y value at an x of 1 is biologically meaningless.

b) b and k are not independent. When, as in this case, x = 1 lies well below the data size range, the correlation of b and k will be strongly negative and this will be a mathematical artifact of the choice of measurement units, for if the units are redefined such that x = 1 now lies above the data size range, the correlation of b and k becomes positive (White and Gould, 1965). That b is a redundant inverse measure of k is demonstrated in Figure 4, depicting the relationship of b and k for 13 samples of *P. cupula.*

Cock (1966) suggests the simple expedient of choosing an x value near the data mean and using $\hat{y}$ (the predicted value of y at this x) as a measure of position. A more meaningful measure for pulmonates is the value of y at an x at the outset of simple allometric growth. When this is expressed in ratio with x, the measure of position also serves as a form ratio giving the basic shell shape at this point. Since the power function applies from whorl 2 onwards, this ratio is defined as HEIGH2-PRHIGH/WIDTH2, the influence of the non-accretionary part of the shell upon its total height again being removed.

The shape of the spire at any point in

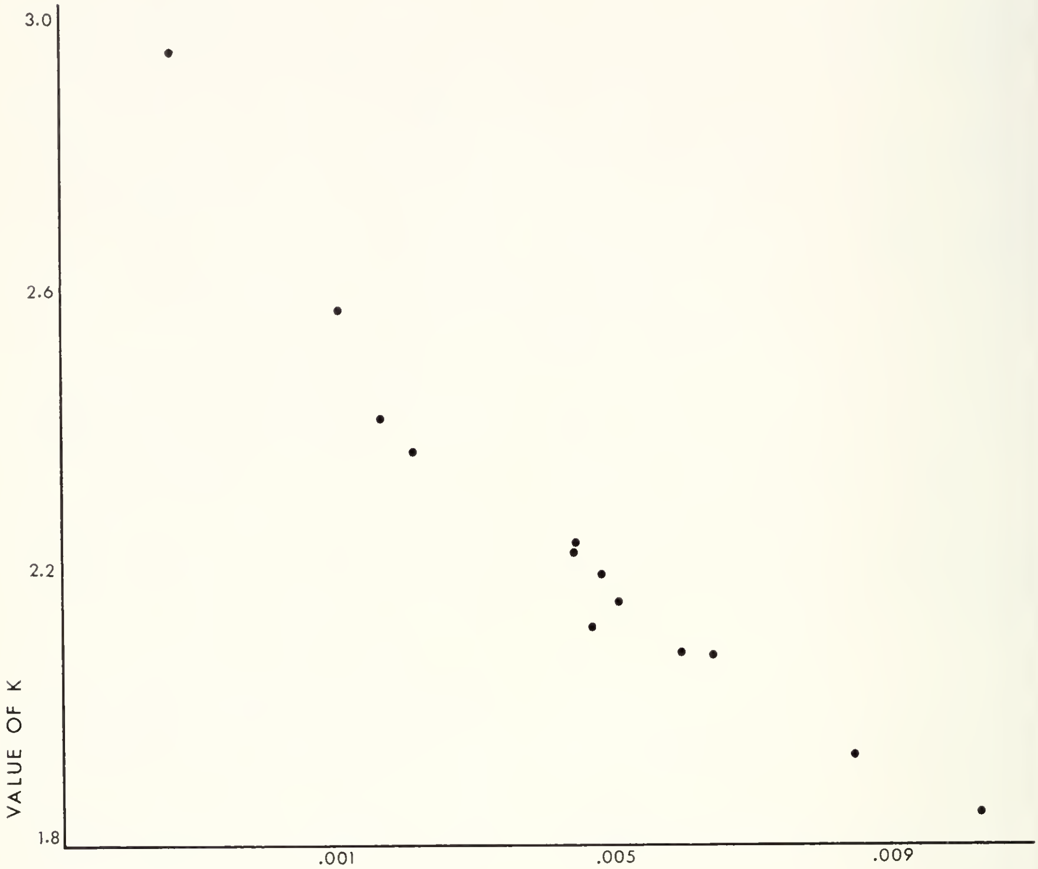

Figure 4. Relationship of b and k among samples of *P. cupula*, illustrating that b is a redundant inverse measure of k for these units of measurement.

ontogeny is a function of three factors: KVALUE, INFORM, and size of the shell at the outset of simple allometric growth (WIDTH2 + HEIGH2):

i) In two shells of identical size and shape at the outset of simple allometric growth, that shell with the higher KVALUE will have a higher and more strongly-domed spire at equal adult sizes because its differential growth of height vs. width was more intense than that of the other shell.

ii) In two shells of identical KVALUE and size at the outset of simple allometric growth, that shell with the higher INFORM will have a higher spire at equal adult sizes because it started simple allometric growth with a higher spire.

iii) In two shells of identical KVALUE and INFORM, that shell which began simple allometric growth at a larger size will, at equal adult sizes, have a lower dome because the same rate of differential increase in height vs. width operated over a smaller range of size.

3. Non-Standardized Variables:

26. Maximum width of the shell, TWIDTH.

27. Maximum height of the shell, THEIGH.

28. Total number of whorls, WHORLS. Measures 26–28 were used as x-values in regressions to obtain standardized values for measures 29–37. By themselves, they do not, of course, appear in the standardized matrices of means.

29. Width of the umbilicus, UMBILC. Predicted values at the standardized size or whorl number for variables 29–37 were obtained by regression.

30. Thickness of the parietal callus, CALLUS.

31. Maximum width of the aperture, APLONG. The apertural measures 31–37 were taken with the shell oriented as follows: perpendicular to the base of the microscope such that the outer whorl periphery (FGC of Figure 2) appears as a line, and rotated dextrally (as the shell grows) to the last point at which the whorl periphery at the aperture (point B) forms the extreme right margin of the field of vision.

32. Maximum height of the aperture, APHIGH.

33. Length of the parietal portion of the inner lip, INNLIP. Line AC of Figure 2.

34. Length of outer lip from posterior extremity of aperture to whorl periphery at aperture, OUTCAR. Line CB, Figure 2.

35. Distance from whorl periphery at aperture to projection of point C upon line AB, UPPOFF. Line C′B, Figure 2.

36. Distance from point A to projection of lowermost point of outer lip upon line AB, LOWOFF. Line AD′, Figure 2.

37. Distance from line AB to lowermost point of outer lip, HALFAP. Line D′D, Figure 2.

4. Measures Derived from Non-Standardized Variables:

38. Ratio of total width to total height, WIDIVH. TWIDTH/THEIGH.

39. Total size of shell, HPLUSW. TWIDTH + THEIGH.

40. Relative width of the umbilicus, RELUMS. UMBILC/HPLUSW.

41. Ratio of apertural width to apertural height, ALDIVW. APLONG/APHIGH.

42. Ratio of aperture height to total height, RELSPI (relative height of the spire). APHIGH/THEIGH.

43. Upper aperture eccentricity, UPPECC. UPPOFF/APLONG (i.e., C′B/AB in Figure 2). When UPPECC = 0.5, triangle ACB is isosceles and the upper part of the aperture is said to be non-eccentric. Deviation from 0.5 in either direction increases the eccentricity which may be positive or negative.

44. Lower aperture eccentricity, LOWECC. LOWOFF/APLONG (i.e., AD′/AB in Figure 2). When LOWECC = 0.5, triangle ADB of Figure 2 is isosceles.

IV. THE ONTOGENY OF *POECILOZONITES*

A) *Principle*

Every measure of shape or color is a function of size in *Poecilozonites*. The ontogenetic relationship between each variable and shell size is allometric.

B) *The Ontogeny of Color*

The treatment of banding as a simple presence-absence phenomenon in pulmonate studies obscures the fact that it has an ontogeny which may be complex. The coloration of juvenile shells is similar in all species of *P.* (*Poecilozonites*); features which distinguish species and subspecies rarely appear before completion of the second whorl. Deposition of color begins on the last 1/2 whorl of the protoconch as even-sided radial stripes, usually four in number and decreasing in width towards the protoconch termination, covering the entire outer whorl surface from its point of contact with the preceding whorl to the umbilicus. After hatching, the even-sided radial stripes continue for approximately one whorl. Gradually the even-sided borders give way to a characteristic zigzag (flame) pattern. (The etymology of *Poecilozonites*, variegated-banded, refers to the zigzag pattern of early ontogeny.) Soon afterwards, constrictions begin to form in the flame in areas of the whorl which will not be banded in the adult. It is only at this point that banding features characteristic of species and subspecies become apparent (recalling von Baer's law of the development of special from general characters). The similarity early in ontogeny of shells which will differ markedly in color as adults has been noticed but not emphasized in studies of other pulmonate genera. Pink ground color is dominant to yellow in *Cepaea nemoralis*, but some pinks develop slowly in ontogeny, gradually masking the yellow color of early whorls (Diver, 1929). Owen (1965) distinguished four morphs (one streaked and three pallid) in adults of the African land snail *Limicolaria martensiana*. The distinctive patterns develop gradually during ontogeny. "The polymorphism is most striking in fullgrown snails, while in snails less than 10 mm long it is difficult to distinguish the pallid forms from each other, and in snails less than 5 mm long it is impossible to distinguish any of the color forms" (Owen, 1965: 374).

The constrictions become more and more pronounced and may even become complete, breaking the flame into segments. In the presumptive band regions, meanwhile, the flame segments become wider and begin to approach each other. The formation of the solid band is not, as Pilsbry (1888: 289) believed, a simple matter of flame coalescence, however. The flames do become relatively wider, but interstitial color is also laid down between the flame segments in the presumptive band areas. The formation of the solid band is a result of both processes.

The species of *Poecilozonites* do not exhibit the impressive array of color and band patterns shown by such highly polymorphic genera as *Liguus*, *Partula*, or even *Cepaea*. Band color is invariably chestnut brown and although bands may vary greatly in width and intensity of coloration, their number never exceeds three, and the position of these three is invariant: two on the upper whorl surface (one below the upper periphery, the other just above the lower periphery) and one just below the whorl periphery. In addition, there may be a supplementary wash of color (not a true band, for it lacks a previous flame stage and has no definable borders) between the subperipheral band and the umbilicus.

The order of flame-band transitions is invariant and occurs, so to speak, from the bottom up. The subperipheral band always forms first, the band above the lower whorl periphery next and the uppermost band last. Moreover, all the bands continue to increase in relative with during ontogeny, the uppermost band doing so fastest of all. If growth continues sufficiently, the bands fuse.

I have adopted a coding system for banding patterns based upon that used by students of *Cepaea*. Starting from the upper whorl periphery, the uppermost band is 1, the band above the lower periphery 2, the subperipheral band 3, and the supplementary color wash above the umbilicus S (for it is not a true band). If the flame-band transition has not occurred by the fifth whorl, a superscript "f" is added after the number of the band. If, as in some forms of *P. cupula*, a band is less than 1/10 the whorl width (at which point it would customarily be called a "line" rather than a band), a superscript "n" is added after the number of the band. If a band is completely absent at the fifth whorl, its position is recorded as 0. (In *Cepaea*, 0 implies that no aspect of the band ever forms. This never happens in *Poecilozonites*. Flame predecessors of the band always appear on the early whorls, but in some morphs, the flames, rather than increasing in strength, become gradually weaker and are finally effaced. When the supplementary color wash is absent, no 0 is recorded because it has no flame stage.) Bands which are fused by the end of the fifth whorl are enclosed in parentheses. Thus, when a specimen has three discrete bands and a supplementary wash at the end of the fifth whorl, it is recorded as 123S (a common pattern for *P. bermudensis zonatus*). If the upper band has yet to form (flames being present), the second band is less than 1/10 the whorl width, the third band is normal, and the supplementary wash absent, the shell is coded 1^f2^n3 (one of the morphs of *P. cupula cupuloides;* another morph of the same subspecies lacks all but the upper band and is coded 100).

In conclusion, the ontogeny of banding in *Poecilozonites* is marked by a gradual and continual increase in the intensity of coloration. This increase is manifested in two ways: by the transition from intermittent flammules to a solid band and by the increase in relative width of the bands, often resulting in their eventual fusion.

C) *The Ontogeny of Shape*

The complexity of allometric trends in the ontogeny of *Poecilozonites* results primarily from the interplay of two factors:

1. "Nucleating" influence of the protoconch: The protoconch of *Poecilozonites* forms within the egg. The adaptive significance of its shape is probably related to functional and mechanical pressures not relevant to later accretionary growth. Its basic shape, therefore, may be expected to bear little relation to those shapes produced by developmental trends operating during the post-embryonic life. Yet the protoconch is a nucleus about which the post-embryonic shell must form and, like the cubic nucleus of a spherical concretion, its influence will not be overcome until the shell has built out a fair distance from it.

Two features of protoconch form are especially relevant to its nucleating influence (Plate 3, Figs. 6–7):

a) It has a very low spire.

b) The aperture is high and narrow.

Upper and lower apertural eccentricities (see Chapter 3, section C, items 43 and 44) are very strong (LOWECC and UPPECC measuring close to 0.0). I suspect that mechanical limitations of space within the egg largely determine the protoconch's quadrate, blocklike shape.

2. Influence of doming in post-embryonic growth: Post-embryonic growth begins with a strong increase in relative width, gradually converting the quadrate protoconch to the wide, low shape characteristic of early whorls. As growth proceeds, the effects of doming become dominant; growth in height exceeds that of width, height of the spire increases relative to height of the aperture, and the shell becomes relatively higher. Three stages in the ontogeny of the aperture and spire may be defined:

a) protoconch: low spire, relatively high aperture, low width/height

b) intermediate: low spire, relatively wide aperture, high width/height

c) maximum size: high spire, relatively high aperture, low width/height.

The similarity of protoconch and adult in some measures of gross morphology does not indicate any functional similarity, since the resemblance is attained in different ways. (A relatively high aperture determines the low width/height ratio of the protoconch; the same low ratio in a large shell is mainly a function of spire height.) The loss and reacquisition of certain shapes do, however, lead to complex bivariate trends in ontogeny. Take, for example, the relationship of aperture length and aperture height[1]. Figure 5 depicts this relationship for an average specimen of *P. bermudensis zonatus*. The concave upward trend of the curve reflects the doming influence in post-

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[1] This relationship should be studied longitudinally (as it develops in single specimens) not cross-sectionally (inferred from mass curves in which each point is a specimen). This can be done by measuring a large specimen and then carefully breaking off a section at a time to obtain points for earlier ontogeny. Since the incremental striae represent former apertural positions, the shell can be trimmed back quite precisely to any of its former apertures.

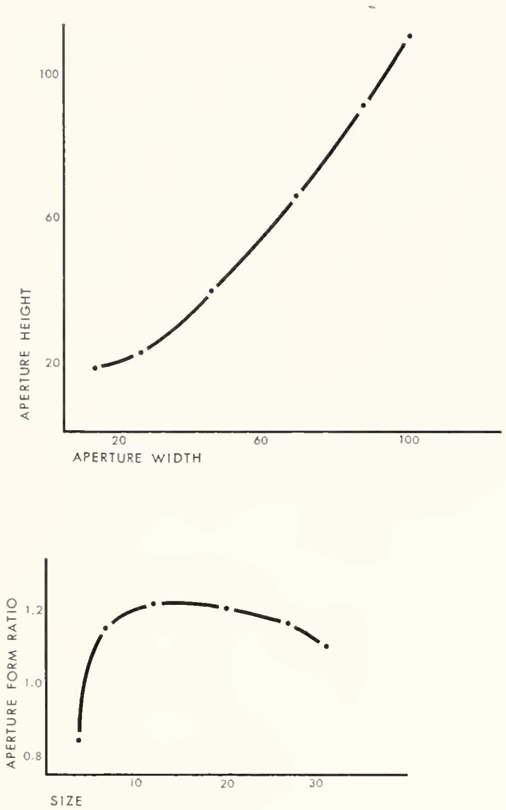

Figure 5. The determinants of ontogenetic allometry: "nucleating influence" of protoconch and doming in post-protoconch ontogeny. Longitudinal data based on a single *P. bermudensis zonatus* from Government Quarry. Pattern completely general for the genus. 5a (above) in micrometer units at 1 unit = .0727 mm. 5b (below) in mm.

protoconch growth; the increase of height relative to width is evident in the form of the curve. If this curve had its origin at (0,0), the ontogeny of the apertural form ratio would be simple: the relative height of the aperture would increase in an even fashion. Due to the nucleating influence of the protoconch, however, the curve does not begin at (0,0) and the ontogeny of the form ratio is complex (Fig. 5b). There is, at first, a sharp *decrease* in relative height as the initial flattened increments are accreted onto the high protoconch. This decrease is not reversed until the third whorl, when the doming trend bcomes dominant and relative height of the aperture begins to increase.

In the last chapter, the variables of this study were grouped into four categories: standardized, derived standardized, non-standardized, and derived non-standardized. Variables in the first two categories have no ontogeny, though the biological features that they measure may undergo allometric growth. (Although the whorl number of a flame-band transition is a single point with no ontogeny, the transition itself reflects a trend towards increasing intensity of coloration. Although the differential growth ratio is constant for a shell, its magnitude measures the most important feature of post-protoconch allometry — the intensity of doming.)

A variable by variable description of allometry in the ontogeny of non-standardized variables and ratios is presented below:

a) UMBILC: The width of the umbilicus increases rather rapidly to a maximum size, after which it remains constant or, in high-spired shells, decreases by constriction (Fig. 6).

b) RELUMS: The relative width of the umbilicus increases slightly, then decreases evenly throughout growth. RELUMS is a conventional pulmonate measure (used by Pilsbry in his taxonomic studies of *Poecilozonites*), and its use is often justified as a means of obtaining comparisons that will be independent of size. It is ironic that just the opposite effect results from its use in *Poecilozonites.* The raw

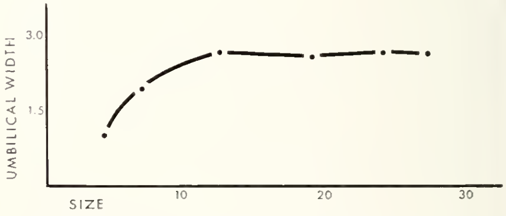

Figure 6. Typical ontogenetic development of umbilical width in *P.* (*Poecilozonites*). Early rapid increase followed by stability. In mm.

measure UMBILC rapidly reaches a maximum dimension which usually remains invariant during growth. When a constant is used as the numerator in a ratio with size, variation of the ratio with growth will be completely due to increase in its denominator, and the stated purpose of the ratio is confounded. For later ontogeny at least, UMBILC itself is the size-independent measure.

c) CALLUS: The parietal callus is absent in *P. cupula*. In *P. nelsoni* and *P. bermudensis zonatus*, it rarely forms until the fourth whorl, thereafter increasing gradually in relative thickness. Complexity is introduced when callus thickening continues during a growth pause; a snail which estivated for several months at whorl 5 and then began to grow rapidly will show an initial decrease followed by the usual gradual increase.

d) WIDIVH: The relative width of the shell increases until the protoconch's influence is overcome; then it decreases gradually (doming effect of post-protoconch ontogeny).

e) ALDIVW: The relative width of the aperture increases sharply at first, then more slowly until the nucleating influence is overcome. Thereafter, as a result of differential increase in shell height measures, it decreases slowly.

f) RELSPI: The spire of the protoconch is virtually flat. Throughout postembryonic growth, height of the spire increases relative to height of the aperture and RELSPI (aperture height/total height) undergoes a regular decrease throughout ontogeny.

g) UPPECC: Increases sharply at first as the flattened early whorls are added to the quadrate protoconch. Thereafter, a slight decrease occurs as the aperture increases slowly in relative height.

h) LOWECC: With RELSPI, the only ratio measure displaying an unreversed trend in ontogeny. Lower eccentricity of the protoconch is 0.0; it increases slowly during ontogeny up to the fourth whorl. During formation of the fifth whorl, a large and rapid expansion occurs (Fig. 7). LOWECC is the only measure of shape which consistently undergoes its most rapid modification during a late stage of ontogeny.

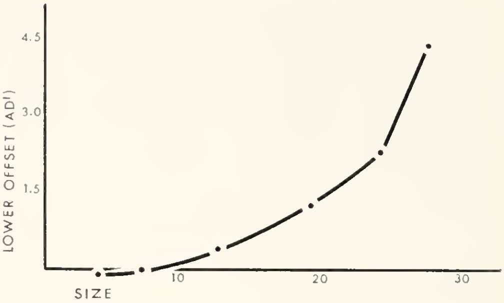

Figure 7. Typical ontogenetic development of lower apertural eccentricity: slow increase followed by rapid increase late in ontogeny. Figs. 5–7 based on the same specimen, which displays patterns completely general for the genus. In mm.

With minor exceptions (*P. cupula* lacks a callus; the umbilicus becomes constricted in high-spired forms), the same ontogenetic trends apply to all species of *P.* (*Poecilozonites*).

V. INTERRELATIONSHIPS OF VARIABLES

> It seemed to the writers, as it has to others, that character changes occurring in evolution of species could not be considered to be independent of each other and that studies which did not consider this dependency ignored a significant aspect of change.
> Olson and Miller, 1958: 1

A) *Factor Analysis*

A matrix of distance measures, itself a major reduction of raw data, is still sufficiently vast in scope to mask patterns of interrelation among many variables. Some technique must be applied to abstract a simpler pattern from the matrix.

Factor analysis, the technique used here, resolves a set of samples (Q mode) or variables (R mode) into a far smaller number of reference axes. Each sample or variable is depicted as a vector; vectors radiate from a common point and the cosine of the angle between any two is a measure of their correlation. Thus, perfectly correlated vectors will overlap (cosine of 0° = 1), while orthogonality (right angle separation) reflects a correlation of zero. Reference axes are constructed within the vector set; various schemes for positioning these axes can be used in the attempt to reach meaningful solutions. In the principal components solution, the first reference axis is that which resolves the most information possible for any single axis. Since the high positive correlation between most body parts in ontogeny is due to the common factor of increasing body size, this axis has been widely interpreted as a general growth factor in R-mode analysis (Teissier, 1948, 1955; Matsuda and Rohlf, 1961; Jolicoeur and Mosimann, 1960; Ouellette and Quadri, 1966). When an orthogonal criterion is maintained for reference axes (mutual orthogonality = mutual independence), other axes are constrained to lie perpendicular to the first principal component. These axes may be mathematical abstractions having no special claim to biological interpretability, and the method has been attacked from this standpoint. If attempts are made to provide the reference axis itself with some biological meaning, this objection is potentially valid. But the axes can also be considered merely as references for defining the positions of vectors within the set. It is in this latter sense that factor analysis is comparable to other multivariate clustering techniques. Thus Boyce (1964), in a Q-mode study of hominoids, used the principal components axes as coordinate systems for a set of two-dimensional slices through the vector swarm. Plots of vector positions on a series of such slices provide a pictorial representation of sample interrelationships that is, in many ways, superior to hierarchical dendrograms (for these give no direct measure of relative distances among individual samples in different clusters). I have used factor axes in this second sense—as references about which vectors may cluster. It is the clustering that demands interpretation. My rationale for rotating the reference axes to positions in coincidence with actual vectors (see next paragraph) is not that the axes then claim greater interpretability, but that they will be more likely to lie near (and therefore serve as references for) groups of associated vectors.

In the varimax solution, reference axes keep their positions relative to each other, but the entire system is rotated within the set of vectors so that the axes fall nearest those vectors which lie at geometric extremes of the vector set. In Q-mode plots discussed in Chapters 6–10, varimax axes are used for coordinate systems. In the oblique solution, used throughout this chapter, the criterion of mutual orthogonality is abandoned and actual vectors lying at extreme positions in the vector swarm are used as reference axes. The final step of each analysis is a matrix whose elements represent the projection of each variable on each reference axis. Each variable is grouped with the reference axis upon which its vector most strongly projects. A reference axis (itself a variable) and its associated variables form a set which may delimit a functional complex of interdependent measures mirroring a common causal factor. Factor analyses were performed on the Columbia University IBM 7094 using Manson and Imbrie's (1964) program COVAP. See Manson and Imbrie (1964), Imbrie and Van Andel (1964), and Gould (1967) for more information on this program.

B) Interrelationships of Variables: Eight Reference Axes

As an example, I shall discuss the oblique projection matrix of a particularly favorable sample. COVAP does not handle matrices with missing data; since approximation was rejected as a source of bias, variables which could not be measured in all specimens were omitted from the analyses. These Government Quarry snails (locality

5) pack a Shore Hills fissure in such abundance that local quarrymen call this area "the graveyard." Preservation is excellent and all variables (with the exception of COLOR3) could be measured in all specimens. Since factor analysis assumes linear relationships among variables, the entire size range cannot be used (see Chapter 4 on complex relationships caused by the protoconch's "nucleating" influence upon early whorls). If the smallest specimens are safely beyond the point of zero slope for non-monotonic relationships, then the linear approximation is sufficiently accurate. The 25 Government Quarry specimens, varying from 23.2 to 37.8 mm in HPLUSW, range in whorl number from 5 to $6\frac{1}{8}$; 45 variables were resolved into 8 reference axes which accounted for 91.3 per cent of the total information.

Interpretation of variable clusters (Table 3):

Axis 1: All non-standardized raw measures with the exception of UMBILC, CALLUS, and UPPOFF, sort with the first axis. In addition, two strongly size-dependent ratios—LOWECC and RELSPI—have their highest projections on this axis (the projection of RELSPI is negative, since its value decreases with increasing size). The biological interpretation of this association is clear: it includes all those measures most strongly correlated with specimen size and is therefore termed the size cluster.

Axis 2: All the standardized measures of early whorl heights sort with this axis. INFORM (HEIGH2-PRHIGH/WIDTH2) includes measures of this group as its numerator; KVALUE projects negatively because high intensity of doming implies a flattened apex and correspondingly low early heights. The association of these variables produces a shell which is relatively high early in ontogeny and, consequently, not strongly domed.

Axis 3: A heterogeneous group of variables sharing the common attribute of tending to produce a relatively wide shell. Although it is a non-standardized variable, UMBILC does not sort with the first axis, because its value is independent of size in the range of this analysis. The form ratio of the shell is the main determinant of its variability; a relatively wide shell mechanically produces a wide umbilicus. WIDIVH, although correlated with size, is in this case more strongly influenced by shape factors tending to produce a relatively wide shell. RELUMS is a redundant measure sorting either with its numerator or denominator. A relatively wide shell tends to be low at late whorl numbers (negative projections of HEIGH5 and HEIGH4), to have a sharp periphery (low PSANGL) and, by definition, a low height/width ratio at standardized whorl numbers.[1]

Axis 4: Standarized widths of later whorls. TSIZE5 includes WIDTH5 as part of its measure. The inclusion of DANGLE, if biologically significant, implies that a shell which is large at a late whorl has a low apertural inclination.

Axis 5: Protoconch width: The inclusion of early whorl widths indicates the extent to which their value is not independent of the protoconch. As more whorls are added, the protoconch width makes up progressively less of the total width and its influence is overcome, usually by the fourth whorl.

Axis 6: LI/CAR (INNLIP/OUTCAR), the reference for this group, is not included in the listing of Chapter 3 because it was found to be a redundant inverse measure of UPPECC. All variables sorting with this axis are related to the upper part of the outer lip of the aperture. OUTCAR,

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[1] As given in Chapter 3, RATIO5 = WIDTH5/HEIGH5. This will be its definition in the matrices of means. In the factor analyses described in this chapter, its value is inverted (height/width). I regret the confusion, but took this expedient because the regression program DASAN printed out height/width ratios at each whorl for each specimen (giving both INFORM and RATIO5).

Table 3. Oblique projection matrix, government quarry sample

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8
WHORLS	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
LOWECC	0.906	–0.088	0.023	0.731	0.140	0.469	0.236	0.497
LOWOFF	0.895	–0.061	0.086	0.770	0.220	0.408	0.097	0.422
INNLIP	0.771	–0.002	0.009	0.570	0.382	0.437	–0.374	–0.260
TWIDTH	0.706	0.011	0.193	0.529	0.318	0.043	–0.305	–0.113
HPLUSW	0.706	–0.009	0.013	0.399	0.330	–0.010	–0.302	–0.223
APWIDT	0.697	0.037	0.165	0.583	0.305	0.040	–0.291	–0.052
THEIGH	0.663	–0.035	–0.232	0.202	0.329	–0.084	–0.280	–0.362
APHIGH	0.587	–0.029	–0.072	0.464	0.350	0.036	–0.379	–0.391
HALFAP	0.516	0.015	0.051	0.499	0.369	–0.114	–0.317	–0.226
OUTCAR	0.515	–0.002	0.011	0.318	0.252	–0.380	–0.263	–0.178
RELSPI	–0.641	0.048	0.456	0.344	–0.073	0.230	–0.086	0.101
TOTECC	–0.803	0.043	–0.043	–0.657	–0.099	–0.084	–0.210	–0.464
HEIGH1	0.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000
HEIGH2	0.054	0.922	–0.243	–0.067	0.058	–0.067	0.004	–0.341
PRHIGH	0.164	0.911	0.220	0.247	–0.262	–0.084	0.282	0.470
INFORM	0.020	0.827	–0.388	–0.226	–0.063	–0.040	–0.009	–0.523
HEIGH3	–0.130	0.724	–0.501	0.008	0.109	–0.294	0.048	–0.429
KVALUE	–0.153	–0.962	–0.060	–0.116	0.331	–0.399	0.154	0.292
UMBILC	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000
WIDIVH	–0.337	0.116	0.813	0.351	–0.173	0.213	0.073	0.576
RELUMS	–0.531	0.025	0.660	–0.316	–0.207	–0.003	0.207	0.171
HEIGH5	–0.181	0.076	–0.639	0.491	0.466	–0.368	–0.274	–0.548
HEIGH4	–0.252	0.357	–0.710	0.112	0.435	–0.424	–0.116	–0.589
PSANGL	–0.174	–0.435	–0.898	–0.435	0.087	–0.288	0.101	–0.703
RATIO5	–0.171	0.037	–0.925	–0.129	0.160	–0.604	0.095	–0.446
DANGLE	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000
WIDTH5	–0.046	–0.062	0.269	0.846	0.553	0.259	–0.575	–0.324
TSIZE5	–0.128	0.004	–0.190	0.788	0.595	–0.046	–0.503	–0.502
WIDTH4	0.001	–0.166	0.216	0.785	0.643	0.245	–0.467	–0.273
PRWIDT	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000
WIDTH1	0.031	–0.057	0.093	–0.107	0.993	–0.065	–0.127	–0.315
WIDTH2	–0.004	–0.157	0.132	0.220	0.957	–0.018	–0.260	–0.284
WIDTH3	–0.117	–0.170	0.164	0.469	0.911	0.101	–0.426	–0.305
LI CAR	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000
UPPOFF	0.447	0.070	0.133	0.349	0.145	–0.531	–0.152	0.048
UPPECC	0.111	0.088	0.062	0.112	–0.051	–0.928	0.027	0.128
COLOR4	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
COLOR5	0.132	–0.098	–0.109	–0.103	–0.032	–0.056	0.894	–0.254
PRDEGR	0.236	–0.056	–0.088	–0.014	0.495	0.092	0.525	0.071
LOWCOL	0.093	–0.052	–0.180	0.233	–0.243	–0.347	0.383	–0.303
ONSELO	–0.393	–0.159	–0.071	–0.197	0.624	–0.285	–0.703	0.373
ONSEUP	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000
ALDIVW	0.397	0.194	0.670	0.362	–0.130	–0.016	0.225	0.870
CALLUS	0.258	0.080	–0.573	–0.011	0.109	–0.137	–0.463	–0.729

another variable in morphological proximity to these, sorts with the size axis (though more weakly than any other variable of that group), but also projects fairly strongly on axis 6.

Axis 7: Color: All but one of the color measures sort with axis 7 as a discrete group. Band onsets (ONSELO) correlate negatively with variables measuring the relative width of color bands. ONSELO is the whorl number of a flame-band transition; the transition occurs at a high whorl number if coloration is weak. The weak sorting of PRDEGR with this axis is probably spurious; it projects almost as highly upon the PRWIDT axis.

Axis 8: A difficult axis to interpret. The association of a relatively wide aperture and a weak callus could record the effects of size (both are characteristic of small specimens). The inclusion of ONSEUP is confusing; weak color is also a feature of small specimens, but ONSEUP is a standardized variable and cannot directly reflect size. CALLUS might be expected to sort with the first axis, but variation in its thickness due to growth pauses (see Chapter 4) is sufficient to mask the weaker correlation with size. The callus is already fairly well developed by the fifth whorl; if a wider size range were used in this analysis, the primary correlation with size would assert itself. The eighth axis accounts for only a small part of the total information and its associations are probably not significant. Nonetheless, the use of many axes may define weak associations which are otherwise overwhelmed by such dominant factors as size.

The status of ALDIVW illustrates the caution with which data of this type must be approached. In longitudinal studies ALDIVW always declines during ontogeny, although that decline is slight. Here, however, the projection of ALDIVW on the size axis is weak but *positive*. The data used for these analysis fall into the "mixed cross-sectional" category of Cock (1966). One set of measures is made per specimen and no age criteria are available. "Variation in size and shape at a fixed age, and variation due to age are inseparably confounded" (Cock, 1966: 236); ontogeny may be poorly represented, or even misrepresented, by such data. Figure 8 depicts the relationship of ALDIVW vs HPLUSW for 46 specimens from Government Quarry. If the entire size range is considered and the circled points ignored, the mixed cross-sectional trend faithfully represents the negative correlation of individual ontogeny. When the size range is compressed, the influence of the static component (that due to variation at a given size) increases and, in this case, actually reverses the correlation. The largest specimens of most *Poecilozonites* samples tend to be relatively wide. When the circled points (7 of the 10 largest specimens) are included and only those specimens reaching 5 whorls considered, the correlation becomes slightly, though insignificantly, positive.

In conclusion:

a) Absolute size is the dominant factor in relationships among non-standardized variables and the measures derived from them. Only two complexes of non-standardized variables fail to associate with the size cluster—those dealing with relative width of the shell and the upper part of the outer lip of the aperture.

b) Of standardized variables and their derived measures, the following is noted:

i) Heights and widths sort separately. There is, moreover, a tendency for their assortment into four clusters: early heights, late heights, early widths and late widths In this analysis

1) early heights are associated with measures of doming intensity.

2) late heights group most strongly (negatively) with variables producing a shell of high relative width.

3) early widths (the value of which includes the protoconch width) sort with the protoconch width.

4) the later widths constitute a separate assemblage.

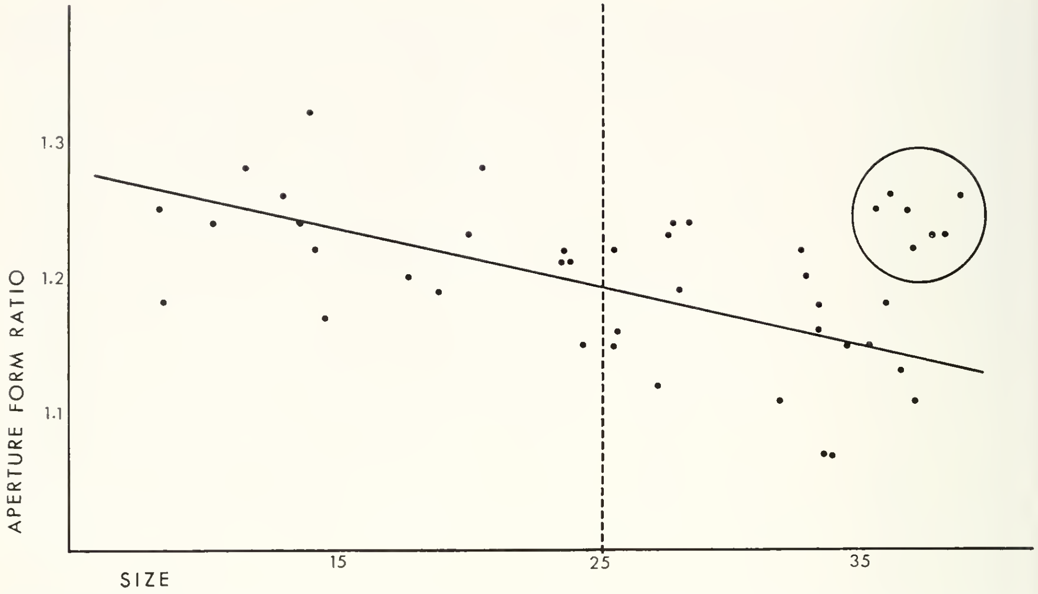

Figure 8. Apertural form ratio vs. shell size for all measured specimens of the Government Quarry sample of *P. bermudensis zonatus*. Consult text for interpretation of regression and circled points. Dotted line separates specimens of five whorls or more from specimens of smaller whorl number. The factor analysis described in text considered only those specimens reaching five whorls.

ii) Color measures sort as a discrete cluster.

C) Hierarchy of Interdependence: Successive Reduction of Axes

The 8-axis scheme is a horizontal transect through a hierarchical structure of interrelationships. It displays a set of groupings at a pre-set level of resolution but gives little information on the relative independence of clusters. Taking non-standardized variables, for example, we find that size exerts a controlling influence. A most important facet of the search for explanation involves a vertical question not answered in a single analysis: What is the hierarchy of size dependence? What groups of non-standardized variables are most strongly size-independent and why? "Most structures tend to contribute to total body size by increasing in dimensions during ontogeny. It is of interest to determine whether this influence is dominant, overshadowing the effects of function and other possible factors" (Olson and Miller, 1958:86). The authors of this passage have used their techniques of "morphological integration" to approach such questions. By successively lowering the level of correlation defining basic groups, clusters which were discrete at higher levels merge in gradual sequence. In the frog *Rana pipiens*, for example, forelimb and hindlimb complexes are separate at the highest level used; at lower levels these unite to form a single association of locomotory measures. The vertical dimension is obtained in a different and only roughly analogous way in this study—by a successive reduction of reference axes. The sequential elimination of axes accounting for the least amount of information causes groups to merge in patterns that reflect the relative importance of various determinants of shell form. Successive reductions to one factor were performed on the Government Quarry sample with the following results:

7 axes: Axis 8 of the previous analysis

is dispersed. CALLUS and ALDIVW join the "relatively wide shell" variables of axis 3. A relatively wide shell tends to have a relatively wide aperture and a weak callus. ONSEUP now groups (negatively) with the "wide at later whorls" axis 4, but its projection on the "color" axis 7 is only slightly weaker. RELUMS has moved to the size cluster (axis 1), HEIGH4 now correlates most strongly with heights of earlier whorls (axis 2); HEIGH5 sorts with WIDTH5. WIDTH2 and WIDTH3 move to axis 4, leaving WIDTH1 to sort with the protoconch width. PRDEGR now groups with PRWIDT. Two of the color measures (COLOR4 and COLOR5) are incorporated into the protoconch width group. The seven clusters are interpretable and, judging from the minimal amount of subsequent shifting, quite stable. As values of the variables increase, the seven clusters produce:

1. a large shell
2. high early heights and low doming intensity
3. a relatively wide shell
4. wide (and large) shell at later whorls
5. a large protoconch and strong coloration
6. a large outer apertural lip
7. a strongly colored shell

6 axes: The color group is eliminated and its members allocated to the third axis. In addition, COLOR5 shifts to the third axis, leaving COLOR4 with the protoconch width group. The signs of vector projections on axis 3 are reversed. The same variables are involved, but increase in their values now produces a relatively high shell. More generally, the third axis variables are a group determining the form ratio of the shell. They are related more strongly to shape at a given size than to size itself. (Since shape is a function of size, this distinction may seem unwarranted, but most of these variables are standardized and unrelated to size.)

1. a large shell
2. high early heights and low doming intensity
3. a relatively high and strongly colored shell
4. wide (and large) shell at later whorls
5. a large protoconch and strong coloration
6. a large outer apertural lip

5 axes: The last discrete group of non-standardized variables is incorporated in the first (size) axis. CALLUS and UMBILC, which show no correlation with size in this sample, are now the only non-standardized raw variables not grouped with the first axis. In addition, two non-standardized ratios (the shell and apertural form ratios WIDIVH and ALDIVW) sort with the "shape" axis 3.

4 axes: The two width clusters (whose references were, respectively, protoconch width and width at the fifth whorl) are combined into one set. COLOR4 joins the third axis cluster and all color measures are now aligned in this group. Four axes account for 75.3 per cent of the total information.

3 axes: The standardized widths are absorbed into the first axis assemblage. HEIGH4 and HEIGH5 now sort with the "relatively high shell" axis 3.

2 axes: All measures of standardized and relative height are conjoined in a second axis cluster. Non-standardized size measures and standardized widths sort with the first axis. Two axes account for 59.1 per cent of the total information.

1 axis: COVAP cannot rotate a single axis (rotation would serve little purpose in any case). This axis is the first principal component, which is, in this case, a general size factor accounting for 42.0 per cent of the total information. If each variable is ranked according to the percentage of its information accounted for by this axis, a chart of relative size dependency results. Two such charts are presented in Table 4, one for Government Quarry, the other for 29 specimens of *P. bermudensis fasolti*

Table 4. Percentage of information accounted for by first principal component (general size factor). Non-standardized raw variables indicated (*), non-standardized ratios as (#).

A) *Government Quarry Sample*

*HPLUSW	0.905	#RELSPI	0.350
*THEIGH	0.899	*CALLUS	0.334
*APHIGH	0.889	#LI/CAR	0.332
*HALFAP	0.877	RATIO5	0.312
*OUTCAR	0.853	PRWIDT	0.311
*TWIDTH	0.838	LOWCOL	0.293
*APWIDT	0.829	DANGLE	0.292
*INNLIP	0.739	PRDEGR	0.286
*UPPOFF	0.694	WIDTH5	0.281
HEIGH5	0.683	ONSEUP	0.222
#TOTECC	0.670	COLOR5	0.220
*LOWOFF	0.656	HEIGH3	0.154
TSIZE5	0.610	COLOR4	0.099
#RELUMS	0.581	PSANGL	0.085
*WHORLS	0.580	ONSELO	0.081
#LOWECC	0.534	HEIGH2	0.064
WIDTH2	0.491	KVALUE	0.025
WIDTH1	0.431	INGRIN	0.023
HEIGH4	0.431	*UMBILC	0.008
WIDTH3	0.372	#ALDIVW	0.001
#WIDIVH	0.369	HEIGH1	0.000
WIDTH4	0.366	PRHIGH	0.000
#UPPECC	0.353		

B) *Tom Moore's Cave Sample,*
P. bermudensis fasolti

*HPLUSW	0.973	WIDTH3	0.167
*TWIDTH	0.970	WIDTH4	0.141
*APLONG	0.963	WIDTH2	0.115
*THEIGH	0.954	PRDEGR	0.082
*INNLIP	0.934	TSIZE4	0.080
*APHIGH	0.897	*UMBILC	0.045
#RELUMS	0.869	PRHIGH	0.022
*WHORLS	0.813	KVALUE	0.011
*OUTCAR	0.806	INGRIN	0.011
#WIDIVH	0.804	HEIGH3	0.010
#LOWECC	0.470	HEIGH4	0.008
#RELSPI	0.450	RATIO4	0.007
#UPPECC	0.318	HEIGH2	0.005
PRWIDT	0.262	#ALDIVW	0.004
WIDTH1	0.244	HEIGH1	0.003

from locality 53. The large size range (16.5–37.7 mm HPLUSW) of this latter sample is especially conducive to the assessment of size dependency.

Table 5. Correlation matrices of standardized widths and heights

A) *Government Quarry Sample,*
P. bermudensis zonatus

	HEIGH1	HEIGH2	HEIGH3	HEIGH4	HEIGH5
WIDTH1	–0.040	0.107	0.160	0.441	0.529
WIDTH2	–0.212	–0.070	0.027	0.378	0.591
WIDTH3	–0.290	–0.193	–0.091	0.279	0.550
WIDTH4	–0.353	–0.270	–0.171	0.177	0.523
WIDTH5	–0.318	–0.268	–0.171	0.135	0.474

B) *South Shore Local Population,*
P. cupula cupula

	HEIGH1	HEIGH2	HEIGH3	HEIGH4	HEIGH5
WIDTH1	0.211	0.368	0.505	0.540	0.550
WIDTH2	0.134	0.296	0.435	0.519	0.598
WIDTH3	0.099	0.257	0.378	0.519	0.652
WIDTH4	0.073	0.200	0.296	0.394	0.578
WIDTH5	0.071	0.183	0.214	0.248	0.334

From the successive reduction of factor axes, I conclude:

a) The strong relative independence of a group of non-standardized variables related to the upper part of the outer apertural lip is confirmed. These are not incorporated into the size grouping until axes are reduced to 5. Of the non-standardized variables and their derivatives, only UMBILC and ALDIVW are virtually size-independent (the first principal component accounts for less than 0.05 per cent of their information in both samples of Table 4). In the case of ALDIVW, this lack of correlation with size is an artifact of the use of mixed cross-sectional data to approximate ontogeny.

b) Of all standardized variables, early heights are most consistently independent of size; protoconch and whorl widths display a small size contingency. This situation is clarified in Table 5, which presents matrices of correlation coefficients among standardized widths and heights for the Government Quarry sample and for a collection of 35 specimens of *P. cupula cupula* from locality 41.[1] The widths of early whorls correlate strongly and positively with heights of later whorls (r of WIDTH1 through WIDTH4 with HEIGH5 is significant at the 1 per cent level in all cases). Early whorl heights, on the other hand, show no correlation (usually insignificantly negative) with later widths. (The correlation of widths with widths and heights with heights is not shown, but is always positive.) Thus, a shell which is *wide* at an early whorl tends to be *large* at a later whorl, while a shell which is *high* at an early whorl tends to be *relatively high but not necessarily large* at a later whorl. If each shell has an equal chance of reaching the same final whorl number, then a shell which is large at the end of the first whorl is likely to be absolutely large at its terminal size. Thus, early widths will bear some relationship to absolute size, while early heights will not.

c) When the discrete color cluster is dispersed by elimination of its axis, the color measures group either with variables related to a relatively high shell or to wide early widths. The previous discussion provides an interpretation for this tendency. Wide early widths imply a relatively high shell at large sizes; such a shell, it would appear, also tends to be strongly colored. With rare exceptions (visual predation of *Cepaea* by thrushes), the adaptive significance of molluscan color patterns is unknown. The discovery of morphological features to which these patterns relate opens the possibility of interpreting evolutionary changes in coloration as pleiotropic responses allied to morphological modifications.

D) Consistency of Results in Other Samples

In order to determine the generality of conclusions based upon the Government Quarry sample, analyses were performed on 10 additional collections of *P. bermudensis* and *P. cupula* (8 reference axes in each case). Since size exerts a controlling influence upon most non-standardized variables, samples differing in size range were selected. As the size range decreases, the percentage of variation attributable to size in non-standardized measures diminishes and relationships previously swamped by the primary factor of size become apparent.[2] Results of the 10 analyses are presented as a table (Table 6) giving the following information for each sample: number of specimens, number of variables, percentage of total information accounted for by 8 axes, range of specimen size (largest – smallest/largest), percentage of variables grouping with the "size" reference axis, and the interpretation of each reference axis cluster. These interpretations follow:

1. Associations attributable to size differences among specimens: S if one single cluster, WS and HS if widths of non-standardized variables sort separately from heights.

2. Assemblages of non-standardized apertural variables; UAP for measures of the upper part of the outer apertural lip (OUTCAR, UPPOFF, UPPECC). LAP for measures of the subperipheral portion of the outer lip (LOWOFF, LOWECC).

3. Other aggregates, including non-standardized variables:

a) FR (form ratio), a heterogeneous group of variables related to the width/height ratio of the shell at the fifth whorl. FR may include the following: raw non-standardized (UMBILC, since a relatively wide shell has an absolutely wide umbilicus), derived non-standardized (WIDIVH, ALDIVW, and RELSPI, the last because a relatively wide shell has a relatively low spire), raw standardized (PSANGL), and derived standardized (RATIO5).

b) U, the umbilicus, which usually groups in FR, may sort independently.

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[1] The patterns are representative of 10 other such matrices and seem to be completely general.

[2] The factoring of partial correlation matrices (with the effects of size removed) would probably be a better approach to this problem.

TABLE 6. INTERPRETATION OF FACTOR AXIS GROUPINGS FOR 11 SAMPLES OF *P.* (*POECILOZONITES*). Interpretation of columns as follows: 1, subspecies name and locality number of sample; 2, N the number of specimens in the sample; 3, V the number of measured variables; 4, % the percentage of total information accounted for by 8 factors; 5, R the range of specimen size within the sample (largest – smallest/largest); 6, S the percentage of variables grouping with the general size factor; 7–23, column headings are the interpretation of the reference axis (explained in text pp. 441–443), the recorded figure is the number of the reference axis whose accompanying cluster of variables bears the interpretation of the column heading.

Sample	N	V	%	R	S	S	WS	HS	PRW	LW	W	EH	LH	H	FR	UAP	LAP	C	D	U	I	?
P. b. fasolti (53)	29	30	95.3	0.56	30	1			6	3		2	7		4	8		–		5		
P. b. zonatus (5)	25	45	91.3	0.39	29	1			5	4		2	3		3	6		7				8
P. b. zonatus (P1)	11	35	98.8	0.30	26	1		6	2	3		8	4			2	5				7 (ONSEUP)	
P. b. zonatus (6)	20	40	89.9	0.27	18	2			1			4	3		6	7		3		5		8
P. b. zonatus (41)	13	41	93.8	0.21	22	3					2			1			5	7		4	8 (DANGLE)	6
P. b. zonatus (73)	20	38	89.7	0.16	–		6			3				5	1	2	8	4				7
P. b. zonatus (69)	13	40	94.8	0.13	–		2	3	1	6		4	6			5	5	7				8
P. c. triangularis (85)	19	28	93.1	0.46	46	1			5	3		4	2			6		–		7	8 (PRDEGR)	
P. c. cupula (P3)	10	37	98.9	0.32	19	1			7		4			2	2	7	3		3		5 (ALDIVW) 8 (PSANGL)	6
P. c. cupula (41)	35	40	85.8	0.28	18	2			6	1		4	3		3	8	7	6	7	5		
P. c. dalli (4)	15	36	93.2	0.16	–		4	6	7			2	1		3	7	8	5				

4. Standardized widths and heights: 4 axes if early widths and heights sort separately from later widths and heights: EH, PRW (since protoconch width is the dominant influence), EW and LW. 2 axes if all widths and all heights sort together: W and H.

5. Standardized color variables: C.

6. Others:

a) In two cases, the measures of doming, which usually are grouped with early heights, sort with their own axis: D.

b) I ("independent"), single reference axis variables sorting independently of all others. (The "independence" is, of course, only relative since reference axes are not mutually orthogonal in the oblique solution.)

c) ?, Small groups of unclear significance. These are confined to the last three axes and would be dispersed early during a series of successive reductions.

The information of Table 7 supports conclusions derived from the Government Quarry sample in the following ways:

1. Absolute size is the dominant factor in interrelationships of non-standardized variables: As the range of size within a sample decreases, the effect of size upon variable interrelationships declines in the following ways:

a) A smaller percentage of variables sorts with the "size" axis. In *P. cupula cupula* from locality 41, for example, WHORLS (always an important member of the "size" cluster when the range of size is large) associates negatively with later widths. A shell which is large at late whorls will tend to have fewer whorls at its final size.

b) The "size" cluster, which always associates with the first axis when the range of size within a sample is large, groups with progressively lower axes as the size range decreases.

c) When the size range within a sample is small, the widths and heights of size-dependent measures sort separately. This recalls the *Rana pipiens* example cited earlier. Forelimb and hindlimb clusters are lumped together when the level of correlation used to form groups is too low to permit a distinction. Likewise, a wide size range swamps more subtle relationships within the group of measures that it controls. At small size ranges, the dominant effect of size is diminished and the separation of widths from heights is made, just as forelimb and hindlimb clusters of *Rana pipiens* are disassociated at high levels of correlation.

2. Certain non-standardized variables show a high degree of independence from the set of size controlled measures:

a) Measures of the upper part of the outer apertural lip: In 8-axis solutions these form a distinct cluster in all but one of the analyses. Only in the *P. bermudensis zonatus* from locality 41 do these measures sort with the "size" axis.

b) Ratios related to the form ratio of the shell (WIDIVH, ALDIVW and RELSPI): These tend to group with the "size" axis when the range of size within a sample is large, and with the "form ratio" axis when it is small.

c) UMBILC: Virtually size-independent (in the absolute sense), umbilical width constitutes its own axis or sorts with the form ratio assemblage as a mechanical correlate of relative shell width.

d) CALLUS: Absent in *P. cupula*, its associations are very erratic in *P. bermudensis zonatus*, though it never associates with the "size" axis. In four of six cases, it occurs in a group of uncertain significance; it is negatively related to standardized widths in two other instances.

3. Standardized widths and heights tend to sort in four groups:

a) Early heights and measures of doming intensity group together. KVALUE and INFORM sort with early heights in four of ten cases.

b) Protoconch width controls the width of early whorls. Its influence is not overcome until the shell has grown to a size at which the contribution made to the total width by the protoconch becomes negligible. In these analyses, WIDTH1 is invariably associated with the protoconch. In only two of eleven cases has WIDTH2 overcome the protoconch influence to sort with later widths; WIDTH3 sorts with later widths in five cases. WIDTH4 is associated with protoconch width in only one case, WIDTH5 never.

c) Late heights and widths sort discretely or with measures of the form ratio assemblage.

4. In an 8-axis solution, color variables tend to constitute a discrete group. Of all morphological features, they show their strongest relationship with the wide protoconch and relatively high shell groups. This conclusion is confirmed in a rough way by these additional data. In six cases, a color measure (or measures) is joined with variables of these groups. This relationship cannot be completely general, however, for in another case (*P. cupula cupula* from locality 41) color measures project *negatively* on the protoconch width axis.

In addition, these data provide new information:

1. Measures related to the subperipheral part of the outer apertural lip also tend to sort independently of size in an 8-axis solution, though their independence is neither as frequent nor as strong as that of corresponding measures of the upper part of the outer apertural lip.

2. A test of redundancy is provided by the observation of invariant similar sorting of a pair or group of variables. RELUMS is a function either of its numerator or denominator. WIDTH1 is invariably related to the protoconch width. PSANGL and RATIO5 measure the height/width ratio at the end of the fifth whorl; only the latter need be used. UPPECC and LOWECC are functions of their numerators; the raw measures UPPOFF and LOWOFF may be considered alone. HALFAP is never independent of the height of the aperture. Sokal (1962) has cited the recognition and elimination of redundancy as a major aim of factor analysis: "Thus the investigator may avoid the redundancy of using characters which only duplicate information already obtained and hopefully approach closer to the ideal of the study of variation

of genetic factors rather than of morphological characters" (1962: 228).

VI. THE EVOLUTION OF *POECILOZONITES CUPULA*

A) The Nomenclature of Diversity

1. *The recognition of P. cupula.* *P. nelsoni* and *P. bermudensis* have long been recognized as major assemblages of wide temporal and geographic extent. Heretofore three minor "species" known from one or a very few localities have been included in the subgenus: *P. cupula* Gulick 1904, *P. dalli* Gulick 1904, and *P. cupuloides* Peile 1924. Collections made from every known snail-bearing locality in Bermuda furnished additional specimens of all three and several new samples that would merit specific distinction under criteria previously employed. Yet the minor types, the new samples, and several collections previously classified as small *P. bermudensis* (in Sayles, 1931) share features of color, form, and distribution sufficient in extent to merit their union into a single polytypic species, *P. cupula*. The diversity of basic form among subspecies of *P. cupula* is great, ranging from 18.4 to 25.5 mm in size at the fifth whorl and from 0.68 to 1.61 in width/height at the fifth whorl, but convergences that continually arise in gross measures of size and shape make these features unsuitable by themselves as criteria for specific discrimination.

Pulmonate systematists have relied heavily upon variation in color banding, at first with "intuitive" feeling for a "good" character, later with the confirmation that banding patterns are often controlled by a simple genetic mechanism—a series of multiple alleles or closely linked genes (Ford, 1964). The basic measures of size and form ratio cannot always distinguish *P. cupula* from *P. bermudensis*, for whereas the latter tends to be larger and relatively wider at the fifth whorl, there is overlap between its smallest members and the largest *P. cupula*. Color patterns, however, permit a complete separation: *P. cupula* displays distinctive band patterns not seen in *P. bermudensis*, never develops a supplementary color wash below band 3, possesses sharp band margins, and never exhibits the "faded" variation (see Chapter 8, section A). No single feature of size or shape can make such a distinction: The parietal callus (absent in *P. cupula*) comes closest; it is invariably present in *P. bermudensis zonatus* but is lacking in its derived subspecies. When all measures of size and shape are considered simultaneously by multivariate methods, virtually complete discrimination is provided.

2. *Infraspecific variation.* One of the most lively issues in pulmonate studies concerns the taxonomic recognition accorded to complex patterns of geographic variation within species. Of *Cerion* in the Bahamas, Mayr and Rosen write: "Every colony appears somewhat different from every other one" (1956: 2). The problem is especially acute in *Achatinella* (Welch, 1938, 1942, 1958) and *Partula* (Crampton, 1916, 1925, 1932); each valley is known to harbor its distinctive population of snails. Such exuberant variation within species led Crampton to establish a hierarchy of infraspecific categories to encompass the diversity. This "scale of subspecific divisions of various grades, down to the groups of individual variants which are essentially identical," (Crampton, 1932: 185) included, in descending order, the variety, socius, cohort, and gens, the last defined as "individuals which are exactly alike in at least one distinguishable character" (1932: 186). Welch erected large numbers of subspecies, relying on a largely arbitrary criterion: "If area A contains shells which are distinct from area B so that the color patterns of the shells can readily be separated 90 per cent to 100 per cent, the demes are considered to be distinct subspecies and given a latin name . . . All demes in which the phenotypes of shells are less than 90 per cent distinct are called microgeographic

races" (Welch, 1958: 130). Such criteria led to the distinction of 78 subspecies and 60 additional unnamed races of *Achatinella apexfulva* (Welch, 1942).

And yet to speak of this infraspecific diversity as a "problem" seems absurd, for it is precisely such morphological variety and its geographic distribution that has provided the major source of information for an understanding of evolution at the species level. It becomes a problem and not a source of delight only when the allocation of names in the quest for an ordering of natural diversity is deemed more important than the search for an understanding of the causes of that diversity. And the former preference seems anachronistic not only in groups for which the so-called "alpha taxonomy" is accomplished, but also perhaps for all infraspecific variation.

Other authors have avoided formal recognition of infraspecific units altogether, hoping thereby to render the evolutionary information more readily accessible. Kincaid, commenting on the work of Welch, writes (1964: 6): "It seems unfortunate that the literature should be burdened with such extensive taxonomic terminology to describe what is essentially an interesting biological phenomenon illustrating one phase of organic evolution. It indicates clearly, however, the difficulty under which taxonomic science suffers in dealing with a problem of this type." Kincaid used the informal term "morph" to delimit 53 demes of the polytypic prosobranch species *Thais lamellosa*. Likewise, Johnston and Selander (1964) have refrained from erecting trinomials for North American house sparrow populations: "Current taxonomic practice gives formal nomenclatural recognition, at the subspecific level, to morphologically definable geographic segments of species populations. . . . Although application of subspecific trinomials to certain New World populations of sparrows would be fully warranted, we are not convinced that nomenclatural stasis is desirable for a patently dynamic system" (Johnston and Selander, 1964: 550).

The primary sin of most infraspecific (and much specific) nomenclature in paleontology has been the naming of mere shapes without sufficient concern for whether the distribution of such shapes is consistent with their existence as a biological population. Thus, the finding that a pulmonate subspecies *alba* is invariably associated with colored shells of similar form should suggest polymorphism within a single population and render a subspecific categorization inappropriate. Each discernible infraspecific unit in *P. cupula*, however, has a geographic range in which it alone resides and a non-disjunct distribution in time—i.e., each distinct morphological entity seems to represent "an aggregate of local populations of a species, inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species" (Mayr, 1963: 348). After presenting this definition of subspecies, Mayr cautions against dignifying each slightly different local population with a trinomial. The diversity in *P. cupula* is so great that every sample displays some characteristic feature of size, shape, or color. To supply each of these with a name would be to construct a static morass of formalized verbiage unapproachable to all but the most specialized readers; and it is, I fear, the wholesale erection of such imposing subspecific arrays that has rendered some of the finest evolutionary works on pulmonate diversity virtually unreadable. To formalize no infraspecific terminology would, on the other hand, be insufficiently expressive of the vast amount of morphological diversity that often prevails within a pulmonate species. Fortunately, a *via media* is available for *P. cupula*—the distinctive individual samples group into well-defined morphological aggregates, each of which, as mentioned above, occupies a range of space and time consistent with that required of the neontological subspecies. Of the five subspecies of *P. cupula* named in this work,[1] three are the degraded species of previous authors and two are new. Only one (*P. cupula dalli*) is known from a single locality. Sylvester-Bradley (1956: 67) has written in his contribution to a symposium on paleontological species: "At one time paleontological research tended ever to promote varietal names to specific level, thereby increasing the burden of nomenclature. Now it is the reduction of a specific name to variety or subspecies that is a sign of increasing knowledge." And Thomas (1956: 27), in the same symposium, writes: "The existence of geographical subspecies in neontology behoves their recognition in fossils."

B) The Description of Diversity

1. *Diversity of Color.* The conservatism of color banding in *P. bermudensis*[2] stands in marked contrast to the variety of patterns known in *P. cupula.* The 21 samples of *P. cupula* may be allocated to two complexes on the basis of a primary dichotomy in banding patterns. The basic stock (*P.c. cupuloides. P. c. triangularis, P. c. dalli,* and *P.c. multispira*) here termed the polymorph complex, is characterized by the following fourfold polymorphism:

a) flames present in the position of band 1 at the fifth whorl, no other color: $1^{f}00$ (see Chapter 4 on band numbering system)

b) flames present in the position of band 1 at the fifth whorl, band 2 absent, band 3 present: $1^{f}03$.

c) band 1 absent, band 2 present (usually as a line), band 3 present; three subtypes (see footnote): $02^{n}3$, 023, and 0(23)

d) flames present in the position of band 1 at the fifth whorl, bands 2 and 3 present; band 2 as a line: $1^{f}2^{n}3$.

The second stock, coextensive with the subspecies *P. cupula cupula*, invariably exhibits a single banding subtype in which all three bands are present, the second as a line: $12^{n}3$. The band pattern of *P. cupula cupula* is most plausibly derived by stabilization of polymorph type d and subsequent intensification of coloration in the band-1 position.

Table 7 summarizes information on color banding for all samples of *P. cupula.* The following information is given: locality, age (refer to Table 1), name of subspecies, color types present in each sample, and number of shells of each type. The distribution of color types within the polymorph complex displays some notable features:

a) The earliest (Walsingham) samples of the polymorph complex exhibit the complete range of shell polymorphism; no younger population displays more than three of the four morphs.

b) The four morphs are ranked in order of increasing intensity of coloration: a (1 flame, no bands), b (1 flame, 1 band), c (2 bands) and d (1 flame, 2 bands). When fewer than 4 morphs are present in the sample, their distribution is always non-disjunct; a and b, b and c, or c and d may occur but never a and c, a and d, or b and d.

2. *Diversity of form.* To provide a picture of the prolific morphological diversity of *P. cupula,* the following account presents the defining features of subspecies and lists the recognizable local populations of each. The basic form of the shell can be encompassed by four measures: the size at the

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[1] Formal taxonomic descriptions will be found in Appendix 1.

[2] Only 023 and 123 and its subtypes are found in *P. bermudensis.* A subtype is defined as a member of a group linked by intermediates within the population. Fused and unfused bands and presence or absence of the supplementary color wash are subtypes in *P. bermudensis*: 123, 1(23), (123), 1(23)S, 123S and 12(3S) (see Plate 5, Figs. 3, 4) are all subtypes of a type. Although direct confirmation is obviously impossible, it is tempting to draw the implication that types are genetically distinct, while variation within subtypes of a type (which vary only in intensity of pigmentation and not in band positions) are either phenotypic expressions of a similar genetic system or under the control of genes whose primary effect is not the regulation of color (e.g., factors controlling the general growth rate).

TABLE 7. GEOGRAPHIC AND TEMPORAL DISTRIBUTION OF COLOR PATTERNS IN *POECILOZONITES CUPULA*. The following information is given for each sample: Loc, the locality number; trivial name of the subspecies; color types present in sample; and N the number of specimens displaying each type.

	Polymorph Complex				*P. cupula cupula*			
Formation	Loc		Color	N	Loc		Color	N
Harrington-Pembroke	84	*multispira*	c) $02^{n}3$	15	35	*cupula*	$12^{n}3$	157
	88		d) $1^{f}2^{n}3$	5	37			
	4	*dalli*	b) $1^{f}03$	8	39			
			e) $02^{n}3$	71	41			
			0(23)	8	43			
			d) $1^{f}2^{n}3$	19	76			
	85	*triangularis*	c) $02^{n}3$	3	77			
			d) $1^{f}2^{n}3$	1	63	*cupula*	$12^{n}3$	11
	46	*triangularis*	c) $02^{n}3$	4				
			023	5				
			0(23)	6				
			d) $1^{f}2^{n}3$	1				
Shore Hills	48	*cupuloides*	c) $02^{n}3$	4	P2	*cupula*	$12^{n}3$	12
			023	1				
			0(23)	8	P3	*cupula*	$12^{n}3$	16
	56	*cupuloides*	a) $1^{f}00$	4				
			b) $1^{f}03$	8				
Belmont	89	*cupuloides*	c) $02^{n}3$	2				
			0(23)	14				
	71	*cupuloides*	c) 023	1				
			0(23)	1				
Walsingham	9	*cupuloides*	a) $1^{f}00$	28				
			b) $1^{f}03$	3				
			c) $02^{n}3$	10				
			0(23)	1				
			d) $1^{f}2^{n}3$	9				
	P4	*cupuloides*	a) $1^{f}00$	22				
			b) $1^{f}03$	6				
			c) $02^{n}3$	8				
			d) $1^{f}2^{n}3$	8				

fifth whorl (S5); the form ratio, width/height, at the fifth whorl (FR5); and the measures of doming intensity (see Chapter 3), the initial form index (InFI) and the differential growth ratio (DGR).[1]

a) *P. cupula cupuloides* (Plate 1, Fig. 3), Walsingham-Shore Hills: Intermediate in all measures of basic form among subspecies of the polymorph complex and geologically oldest, this subspecies may represent the parental stock of all later *P. cupula* subspecies. Several local populations are distinguishable.

i) Quarry Road local population: Shells from Peile's type locality cannot be distinguished from those of the adjacent Quarry Road samples. Both display all four color morphs and almost identical values of the basic form measures (12.1 and 12.0 mm S5, 1.16 and 1.16 FR5, 2.15 and 2.19 DGR, .282 and .278 InFI).

ii) West Coney Island local population: The lighter morphs (a and b) have become stabilized; shells are smaller (S5 = 11.2 mm) and relatively wider (FR5 = 1.30) than those of the Quarry

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[1] Cited figures in this discussion are mean sample value of these variables. A complete account of morphological differences among samples is found in the matrix of means, Appendix 3.

Road local population. Differences among local populations are significant at the 5 per cent level unless otherwise noted.

iii) Surf Bay local population: Morph c alone is present (but only 2 specimens have discernible color markings). The set of means for basic form measures of the 7 specimens is distinct but not significantly different, perhaps due to small sample size, from that of other samples.

iv) Bird's Nest local population: Lowest FR5 (1.07) and correspondingly highest DGR and InFI (2.22 and 0.296) for *P.c. cupuloides* populations. S5 (12.0 mm) indistinguishable from Surf Bay and Quarry Road local populations. Morph c alone is present.

v) Ferry Road local population: 13 specimens with discernible color markings are all of morph c. The poorly preserved specimens were not measured.

b) *P. cupula triangularis* (Plate 1, Fig. 5), Harrington-Pembroke: The low doming intensity of this subspecies (only *P. cupula* with mean sample DGR less than 2.00) imparts a more or less triangular cross section to the shell. Since the initial form index is also low, this subspecies is the relatively widest of all *P. cupula*. Morphs c and d are present in both its local populations.

i) Pink Beach Road local population.

ii) Devil's Hole local population: The Devil's Hole population is larger at the fifth whorl (13.2 vs. 12.1 mm); it has a lower DGR (1.85 vs. 1.94), but the correspondingly higher InFI (.247 vs. .220) produces a form ratio insignificantly different from that of the Pink Beach Road population (1.55 vs. 1.61).

c) *P. cupula dalli* (Plate 1, Fig. 2), Harrington-Pembroke: This population of *P. cupula* is unique among all samples of *P.* (*Poecilozonites*): it is the smallest ($S5 = 9.7$ mm), the relatively highest ($FR5 = 0.68$), and possesses the greatest mean sample values of DGR and InFI (2.94 and 0.418). I have previously noted (Gould, 1966a) that all these features are interrelated. Since progressively larger values of the differential growth ratio imply continually more rapid increases in the height/width ratio during ontogeny, a high differential growth ratio will be size-limiting. A *P. cupula dalli* of just twice maximum width would possess a shell six times higher than wide.

i) Albuoy's Point local population.

d) *P. cupula multispira* (Plate 1, Fig. 4), Harrington-Pembroke: At the fifth whorl, *P. cupula multispira* is no larger than *P. cupula dalli*. Yet large individuals of this subspecies reach sizes unexcelled by any other *P. cupula*. All other populations of *P. cupula* (and of *P. bermudensis*, for that matter) show a surprising stability in average whorl numbers of large specimens (always between 5 and 6½). *P. cupula multispira* is unique in exceeding this number; the largest specimen in my collection has $7\frac{6}{8}$ whorls. Since the largest specimens reach relative heights even greater than that of *P. cupula dalli* at the fifth whorl, A. Haycock (correspondence with E. G. Vanatta in collection of the Philadelphia Academy of Natural Sciences) allocated these specimens to *P. cupula dalli*. Though they overlap in this one feature of form ratio, the two subspecies are as distinct from one another as any two taxa of *P. cupula*, and the misallocation serves to indicate the pitfalls of a single-character taxonomy.

There is an element of mechanical inevitability in the mode of production of certain shapes in accretionary structures. We know that the high spire of large *P. cupula multispira* cannot be attributed to a high differential growth ratio. High differential growth ratios, unless accompanied by a low initial form index or extremely large early whorls (see discussion on doming factors in Chapter 3), are severely size limiting (Gould, 1966a). Since the mean initial form index of *P. cupula multispira* is average for polymorph *P. cupula*, the high dome must be attributed to the third doming factor—extremely small protoconch and early whorls. *P. c. multispira*'s mean differential growth ratio of 2.24 is average for *P. cupula*, but any differential growth ratio greater than 1 implies continual increase in the height/width ratio. *P. c. multispira* is high spired because an average differential growth ratio began operating at an unusually small size. (The differential growth ratio is measured from the termination of whorl 2 to the end of growth; that *P. c. multispira* has an unusually large number of whorls at the size of an average *P. cupula* adult implies, indeed, that the protoconch and initial whorls are small.) Thus, *P. cupula dalli* and *P. cupula multispira* illustrate two of a strictly limited number of pathways to the attainment of a high spire, and the maximum size attained by each subspecies is a function of the chosen pathway.

i) St. David's Island local population: Three localities (84, 88, and 91), the shells of which cannot be distinguished.

e) *P. cupula cupula* (Plate 1, Fig. 1), Shore Hills-Pembroke: The nominate subspecies of *P. cupula* is distinguished from members of the polymorph complex by its unique banding pattern (12"3) and features of morphology discussed below (larger size and different DGR vs. InFI relationship).

i) South Shore local population: Found at five localities (35, 37, 39, 41, 43) along a relatively continuous outcrop of Harrington or Pembroke accretionary zones running for 1700 m along the South Shore from Spencer's Point to Devonshire Bay; also present at two localities (76, 77) on Knapton Hill. Next to largest and relatively widest (a function of lowest DGR and InFI) of the local populations of *P. cupula cupula*, large specimens bear an uncanny similarity to shells of some *P. bermudensis zonatus* samples (the possibility of introgression will be considered in Chapter 10). Sayles (1931) allocated specimens from these localities to *P. bermudensis*.

ii) Gibbet Island local population: Smallest population of *P. c. cupula*; intermediate in other respects.

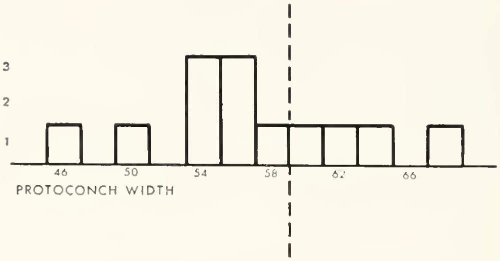

Figure 9. Histogram of mean sample values of protoconch width in *P. cupula* showing complete separation of *P. cupula cupula* from the polymorph complex (left of vertical line). Values on abscissa are midpoints of class intervals (micrometer units at 1 unit = .0327 mm).

iii) Whitby local population: Intermediate in all basic features of morphology, the Whitby population is unique in the narrowness of color band 3. Average relative width for this band is .099, while the range for all other *P. c. cupula* is .166 to .200.

iv) Walsingham local population: These shells from the species' type locality are the largest (S5 = 14.0 mm) and relatively highest (R5 = 0.97) of *P. cupula cupula* samples.

On the basis of color patterns alone, a primary dichotomy was made between *P. cupula cupula* and members of a "polymorph complex" (*P. c. cupuloides*, *P. c. triangularis*, *P. c. dalli*, and *P. c. multispira*). The following differences in size and shape reinforce the validity of this separation.

a) *P. cupula cupula* is larger at the fifth whorl. Of the polymorph complex, only the Devil's Hole local population of *P. c. triangularis* exceeds the smallest *P. cupula cupula* population (Gibbet Island) in S5. There is no overlap in protoconch width; that of the smallest *P. c. cupula* exceeds that of the largest polymorph population (Fig. 9). If we assume that *P. cupula cupula* was derived from *P. c. cupuloides* by stabilization of morph d and intensification of coloration in the band-1 position, then the correlation of morph type and size at the fifth whorl in the Quarry Road

TABLE 8. CORRELATION OF SIZE AND COLOR MORPH TYPE IN THE QUARRY ROAD LOCAL POPULATION OF *P. CUPULA CUPULOIDES*

Morph	a	b	c	d
Mean size at fifth whorl	11.86	12.23	12.13	12.48
Number of specimens	12	3	6	5

local population of *P. c. cupuloides*, shown in Table 8, assumes special importance. The mean S5 for shells of morph d is larger than that for shells of morph a, and the difference is significant at the 5 per cent level ($0.02<p<0.05$; $t=2.29$ at 15 d.f.). That this correlation of size and morph type holds not only within but also among samples is illustrated by the West Coney Island population, which has stabilized morphs a and b and is the smallest *P. c. cupuloides* (S5 = 11.2 mm). The two measured populations of *P. c. cupuloides* which have stabilized morph c are intermediate in S5 (12.0 and 11.9 mm) between the Coney Island snails and morph d shells of the Quarry Road population. Thus, size and morph type are correlated among shells of a population, among populations of a subspecies, and between subspecies of an inferred ancestor-descendant sequence in *P. cupula*. Although the genetic cause of the correlation is probably unknowable,

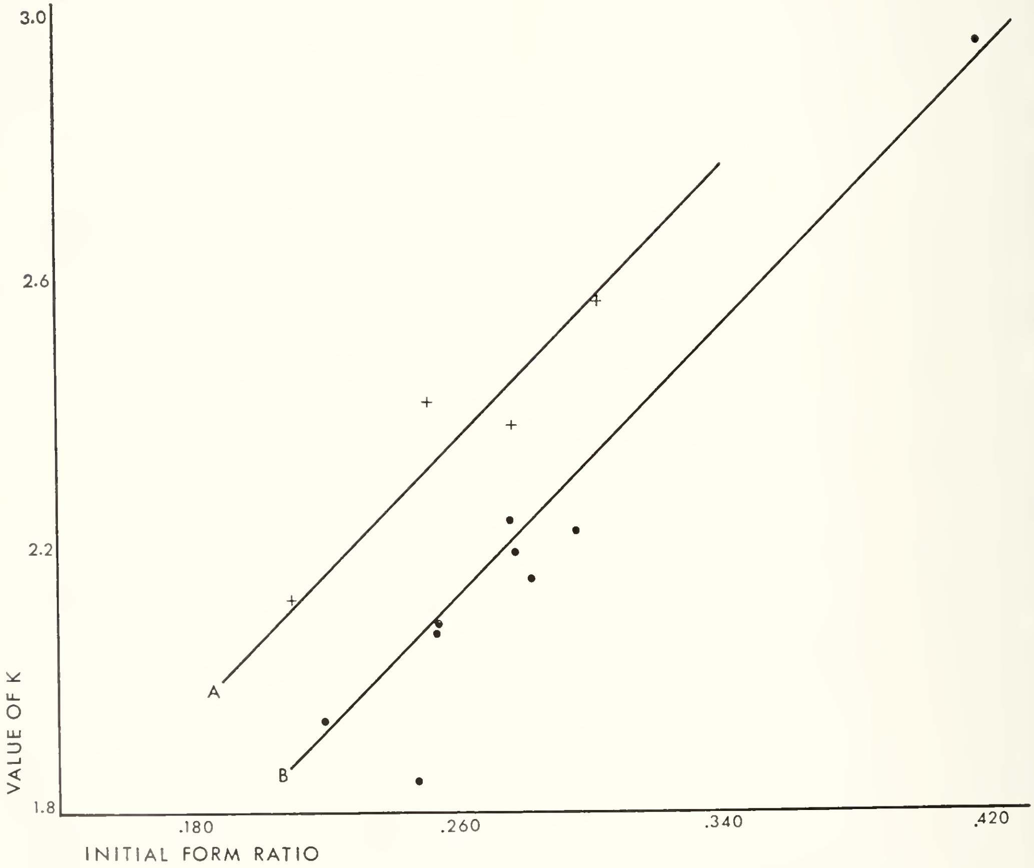

Figure 10. Differential growth ratio vs. initial form index for all *P. cupula* samples. Polymorph complex samples on lower regression, *P. cupula cupula* on upper (with South Shore local population samples grouped as a single grand sample).

this example does demonstrate that color variation may have morphological correlates and that the adaptive significance of a color pattern need not reside exclusively in the pattern itself.

b) Figure 10 shows the relationship between DGR and InFI for mean sample values of all measured *P. cupula* samples. The data are well approximated by two parallel lines for *P. cupula cupula* and the polymorph complex, respectively. At equal values of the differential growth ratio, *P. cupula cupula* tends to have a lower initial form index and, correspondingly, a relatively wider shell than members of the polymorph complex of the same size.

In addition to providing a discriminatory index, this relationship illustrates a point often overlooked in correlation studies. Among individuals of a population, the correlation of InFI and DGR is *always negative* (reaching values as high as -.727 for the *P. c. cupula* South Shore local population, and -.789 for *P. bermudensis zonatus* from Government Quarry). Among populations of *P. cupula*, the correlation is *strongly positive* (r = +.787 for all *P. cupula* considered together and +.971 for populations of the polymorph complex). This discrepancy ceases to be surprising when we realize that the correlation of InFI and DGR is controlled by different factors within and among populations. A negative correlation implies that later growth operates in the opposite sense to previous development. Stabilizing selection within a population will allow a limited range of adult form ratios. If initial growth in relative height is abnormally rapid (high InFI), the DGR will tend to be low in order to produce a final form ratio within the favored range. Unusually low values of InFI will require a correspondingly high DGR. (I infer from its high variability that the DGR is strongly subject to the influence of feedback from early development.) A positive correlation, on the other hand, implies that early and later growth vary together to produce the final shape. If it is selectively advantageous for shells of one population to be relatively higher than those of another, an increase in *both* DGR and InFI will most efficiently produce the higher spire. Among populations differing in mean adult form ratio, a positive correlation is to be expected.

Given these consistent differences in color and morphology, a case could be made for specific distinction of *P. cupula cupula* from the polymorph complex. Yet such a discussion seems vacuous while morphology alone supplies the evidence, and the more conservative view is adopted here.

A multivariate assessment of morphological differences among subspecies is provided by Q-mode factor analytic plots on varimax axes (Chapter 5, section A). The matrix of means, with mean sample values for non-standardized variables given at 5⅜ whorls,[1] was used in the analysis. COVAP does not handle missing data, and all the color measures save relative width of band 3 were omitted, since fewer than five measured specimens provided data for the other color variables in many samples. This elimination has the salutary effect of permitting a comparison of size and shape alone (relative width of band 3 is not a strongly discriminating measure).

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[1] Matrices of means for *P. cupula* and *P. bermudensis*, the epitome of all data used in this work, will be found in Appendix 3.

A whorl number (rather than a size) is used for standardization since the whorl number at maximum size varies very little in *P. cupula;* thus, whorl number approaches the ideal of standardization at a developmental stage. This introduces a serious bias only for *P. c. multispira*, the maximum whorl number of which exceeds all other samples by 2. Many of its values confirm the impression that it is being considered at an earlier developmental stage than are the other samples. Its value of "the lower eccentricity," for example, is the lowest of all samples, but since "the lower eccentricity" is the one non-standardized measure which undergoes its greatest change late in ontogeny, this may indicate only that, at 5⅜ whorls, the *P. c. multispira* sample is developmentally younger than all other samples.

A percent-range transformation was used to eliminate unequal weighting of variables due to differences in their magnitude. (Manson and Imbrie, 1964). Samples are represented on plots by the following numbers:

- *P. cupula cupuloides*
  - i) Quarry Road local population: 13, 14
  - ii) West Coney Island local population: 15
  - iii) Surf Bay local population: 19
  - iv) Bird's Nest local population: 18
- *P. cupula triangularis*
  - i) Pink Beach local population: 11
  - ii) Devil's Hole local population: 12
- *P. cupula dalli*
  - i) Albuoy's Point local population: 17
- *P. cupula multispira*
  - i) St. David's Island local population: 16
- *P. cupula cupula*
  - i) South shore local population: 01, 02, 03, 04, 05, 06, 07
  - ii) Gibbet Island local population: 08
  - iii) Whitby local population: 09
  - iv) Walsingham local population: 10

Figure 11, a plot of axis 1 vs. axis 2 of a 3-axis solution, gives a picture of relative morphological similarity among subspecies as recorded by 32 variables.

a) *P. c. dalli* and *P. c. multispira* are very distinct from all other samples and from each other. Their mutual separation confirms their subspecific status and demonstrates that the similar form ratio of large specimens is a superficial convergence.

b) The local populations represented by more than one sample (Quarry Road *P. c. cupuloides* and South Shore *P. c. cupula*) group as tight clusters in all plots.

c) In the absence of distinctive color variables, the 3-axis plot does not distinguish the samples of *P. c. triangularis* from the South Shore local population of *P. c. cupula* (these are, collectively, the relatively widest samples of *P. cupula*). If a fourth axis is added (Fig. 12), a distinction of the two subspecies is established. Highest projections upon the fourth axis are exhibited by the Whitby and Walsingham local populations of *P. c. cupula*. The South Shore local population projects fairly strongly on this axis, the samples of *P. c. triangularis* very weakly.

d) The three *P. c. cupula* local populations of low fifth whorl form ratio are not well distinguished from the *P. c. cupuloides* cluster in the absence of distinctive color variates. Some weak separation is indicated by the higher joint projections of the *P. c. cupula* samples upon both axes 1 and 2.

Table 9 presents an oblique projection matrix for the 3-axis solution. Again, *P. c. dalli* and *P. c. multispira* are seen to be very different from all other populations and from each other. *P. c. triangularis* is not separated from the South Shore *P. c. cupula*, but the weak distinction of relatively high *P. c. cupula* populations from samples of *P. c. cupuloides* is confirmed by samples of *P. c. cupuloides* is confirmed by the projections of all *P. c. cupula* local populations (higher than that of any *P. c. cupuloides*) upon the sample of the South Shore local population of *P. c. cupula* that serves as the first oblique reference axis.

3. *Distribution of P. cupula in time.* Although temporal and geographic ranges of subspecies can be documented, the arrangement of these populations in a phylogenetic pattern requires some very speculative inference. (The phylogeny of *P. bermudensis*, which, due to far greater sample numbers, sizes and temporal control, can be documented with high accuracy, will be discussed later. The tenuous nature of conclusions concerning *P. cupula* should not be read as a model for the general degree of resolution attainable in these studies.) If the observed ranges represent true ranges, then the following conclusions are probable:

a) *P. c. cupula* arose during Shore

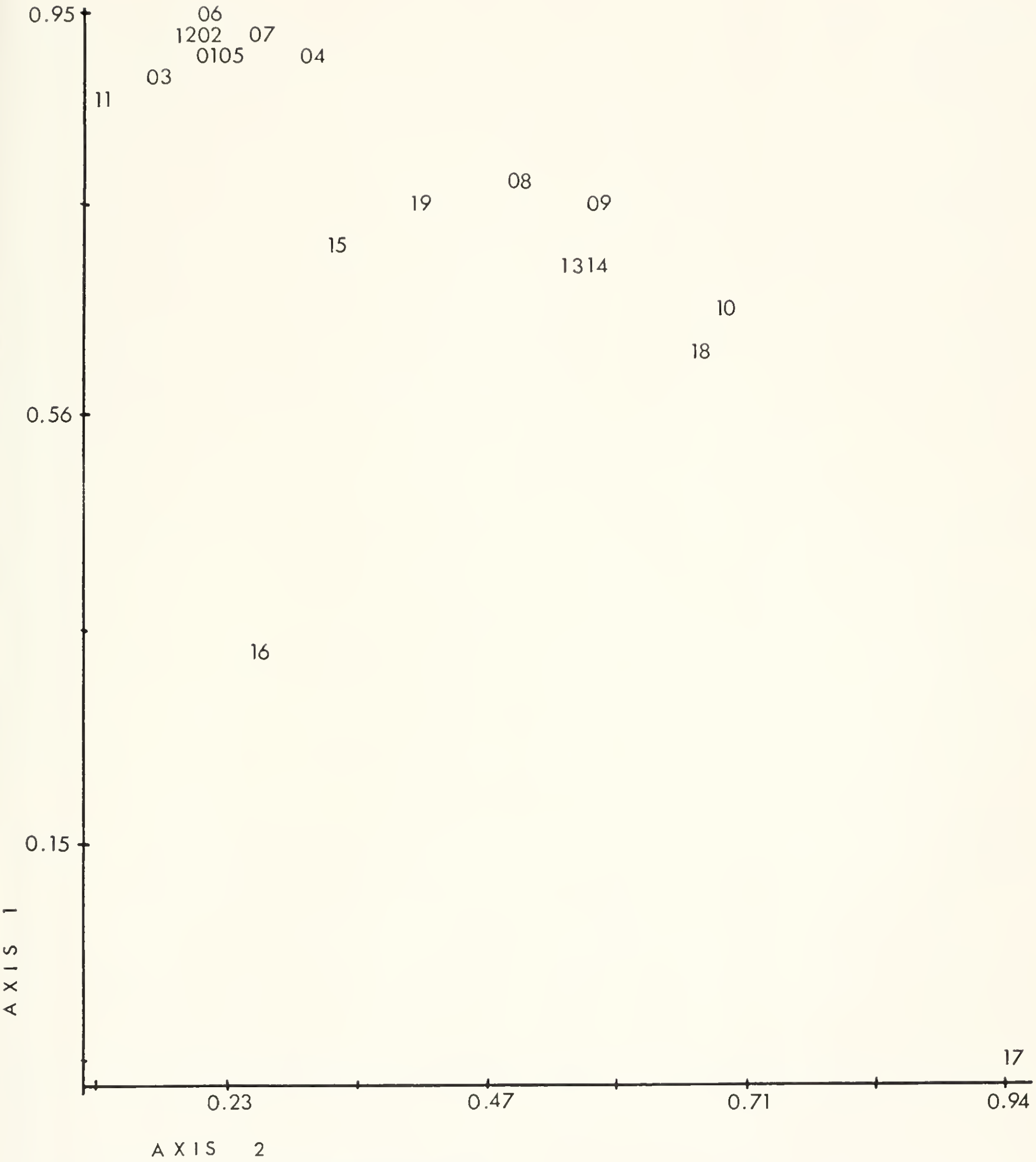

Figure 11. Plot on varimax axes of all *P. cupula* samples.

Hills times from a population (or populations) of *P. c. cupuloides* which had stabilized morph d.

b) The polymorph complex underwent an adaptive radiation, just before the base of the Harrington, which resulted in the extinction of parental *P. c. cupuloides* and the origin of (at least) three new subspecies.

c) All subspecies of *P. cupula* (at least four) became extinct at the top of the Pembroke. Although the first two statements are quite speculative, this third conclusion is well documented. Not a trace

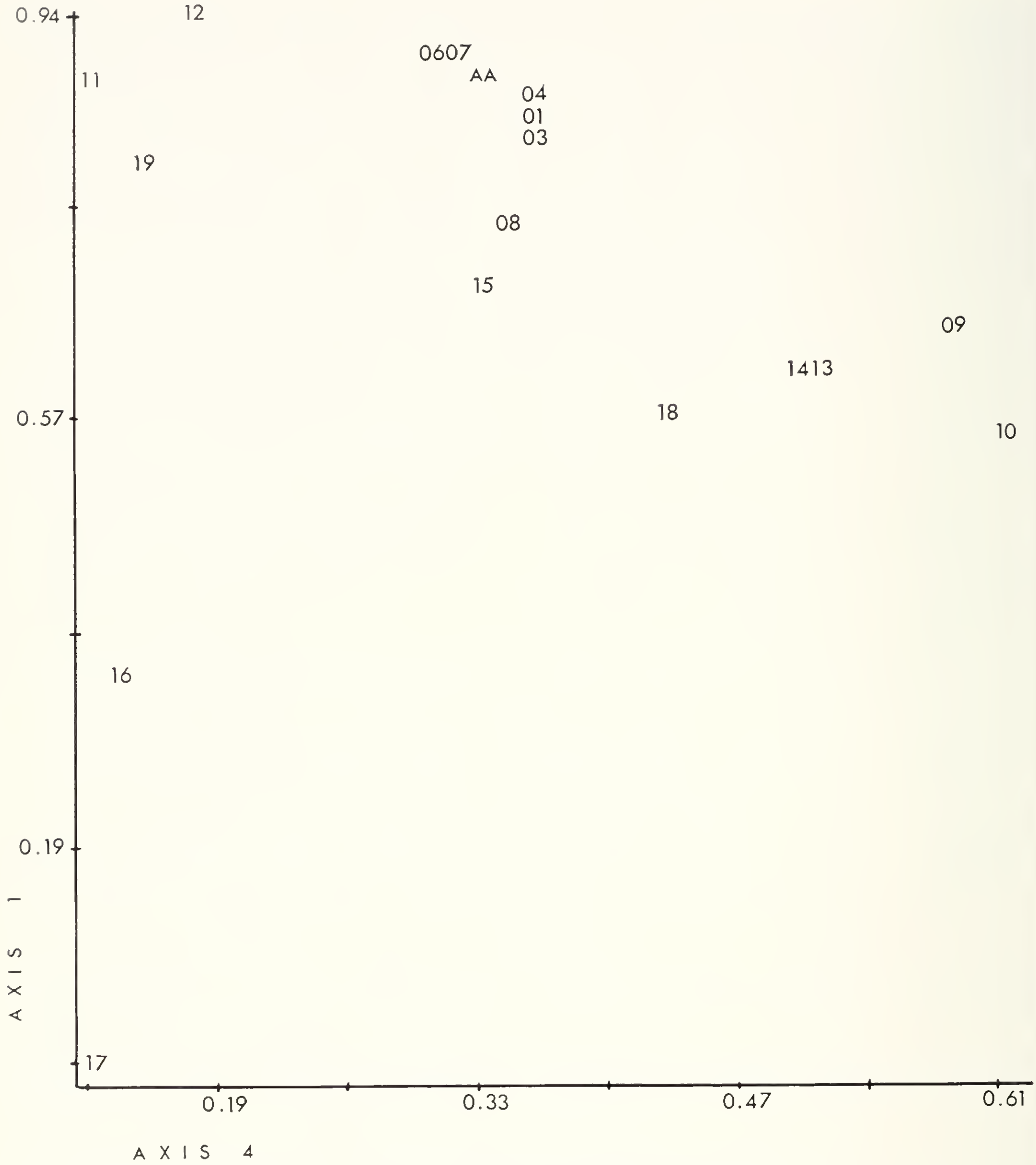

Figure 12. Plot on varimax axes of all *P. cupula cupula* samples. AA stands for 02 and 05.

of *P. cupula* has ever been found in the extensive St. George's and Southampton fossil-bearing formations.

When the subspecies ranges are compared with a chart of inferred sea-level fluctuations (Fig. 13), a basis for interpretation of the phylogeny proposed above is established. The pre-Harrington adaptive radiation is coincident with the rise of the Devonshire sea to a maximum of +5 meters. At such a level, Bermuda would be dissected into even more islands than exist today. A large number of geographically isolated potential habitats

TABLE 9. OBLIQUE PROJECTION MATRIX FOR ALL *P. CUPULA* SAMPLES. The following identifying information is given for each sample: trivial name of the subspecies, name of the local population and locality number when more than one sample of a local population was measured.

Sample	Axis 1	Axis 2	Axis 3
cupula (South Shore, 43)	1.000	0.000	0.000
cupula (South Shore, 41a)	0.987	-0.056	0.050
triangularis (Devil's Hole)	0.967	-0.078	0.057
cupula (South Shore, 41c)	0.950	0.038	0.070
cupula (South Shore, 37)	0.950	-0.080	0.123
cupula (South Shore, 41b)	0.930	-0.051	0.143
cupula (South Shore, 35)	0.895	-0.066	0.194
cupula (Whitby)	0.853	0.380	-0.048
cupula (Gibbet Island)	0.849	0.275	0.039
cupula (South Shore, 39)	0.839	-0.131	0.284
triangularis (Pink Beach Road)	0.813	-0.204	0.320
cupula (Walsingham)	0.792	0.565	-0.141
cupuloides (Surf Bay)	0.767	0.169	0.194
cupuloides (Quarry Road, 9)	0.710	0.332	0.202
cupuloides (Quarry Road, P4)	0.695	0.337	0.216
cupuloides (Bird's Nest)	0.662	0.498	0.104
cupuloides (Coney Island)	0.599	0.031	0.506
dalli (Albuoy's Point)	0.000	1.000	0.000
multispira (St. David's Is.)	0.000	0.000	1.000

would then be available. Rensch (1937) invoked a similar explanation for the diversity of the *Murella muralis* stock in western Sicily. "In the late Tertiary and during part of the Pleistocene, the mountains of Western Sicily were inundated to form islands and peninsulas. Individual mountains were then more strongly isolated than they are today and the stabilization of races was promoted" (translated from Rensch, 1937: 587). The total extinction of *P. cupula* is concurrent with the highest post-Belmont Sea—the Spencer's Point, which rose to +20 meters and virtually inundated the entire island complex. In earlier formations *P. cupula* is often associated with *P. nelsoni; P. bermudensis* rarely occurs with either of the other species of its subgenus. *P. nelsoni* was similarly affected by the Spencer's Point rise, for it is present in the St. George's in only two adjacent localities and is never found in the Southampton. *P. bermudensis*, on the other hand, is quite common in the St. George's and seems to have survived the Spencer's Point inundation with little difficulty. This implies that *P. bermudensis* can adapt itself to dune conditions more readily than other members of its subgenus. Dunes form at the island periphery and, with the drastic reduction of subaerial Bermuda during Spencer's Point time, the remaining land must have been "all periphery," completely effacing the calmer habitats that *P. cupula* and *P. nelsoni* may have preferred.

C) The Cause of Diversity

Adjacent local populations of a pulmonate species are often strikingly diverse, even when a uniform environment seems to prevail throughout the inhabited area. The difficulty of attributing such extreme variability to the effects of natural selection alone has prompted many authors to suggest that random processes of evolutionary change—genetic drift and the founder principle—are acting to initiate, and perhaps even to maintain, the diversity. Mayr and Rosen (1956), commenting on the "crazy quilt distribution pattern" of *Cerion* in Bimini, write: "It is possible and probable that many if not most colonies are founded by a single fertilized adult . . . Each new colony is an evolutionary experiment." At its outset, the new population exhibits gene frequencies different from those of its parental source because the small number of founders cannot be expected to transmit a complete replica of the parental gene pool, but there are also reasons why selection will then promote rapid divergence in a founder population: high inbreeding in early generations, for example, exposes homozygous genotypes to selection more often than in outbred populations (Mayr and Rosen, 1956). Thus, the ultimate genetic separation of the newly-founded and parental populations results both from random genetic attributes of the founders and from

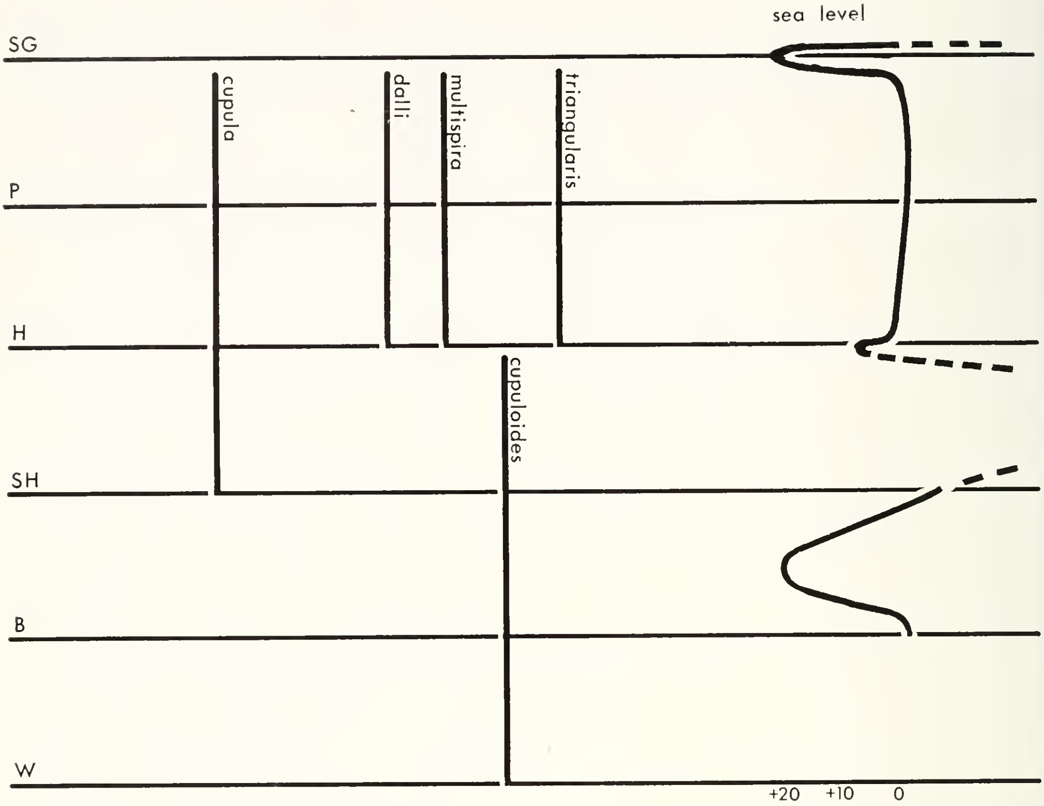

Figure 13. Ranges of the subspecies of *P. cupula*. See text for inferred phylogeny and correlation with rise and fall of Pleistocene sea.

subsequent selection. Komai and Emura (1955) cite the founder principle as "the most important cause of the differentiation of natural populations of this snail [*Bradybaena similaris*]. Besides, there must have been genetic drift due to the small size of breeding population" (1955: 415).

Other authors have responded with a vigorous defense of the total efficacy of selection and some spirited controversies, constituting much of the best recent work on pulmonate microevolution, have ensued. To illustrate the controversy, I have selected the drosophilas of pulmonate microevolutionary studies: *Cepaea* and *Partula*.

a) *Cepaea:* The literature is reviewed by Ford (1964) and Harvey (1964) and will not be extensively cited here. Morph frequencies within populations are known to be strongly influenced by visual thrush predation (cryptic coloration is afforded by different morphs in different environments or during seasonal fluctuations of a single environment), and by varying environmental tolerances of the morphs. Lamotte (1951) maintained that dissimilarities among colonies were due more to genetic drift than to selection, but his reasons have been disputed by later authors. He found, for example, that differences among smaller colonies are greater than among large ones, but Mayr (1963) asserts that more precise adaptation is attainable in the uniform habitats of small colonies. Lamotte found no correlation between morph frequencies of *C. nemoralis* and *C. hortensis* living together on the same background, but Clarke (1960) showed that similar cryptic patterns can be attained by different routes. In uniform beachwoods, where brown coloration is most advantageous, brown unbanded *C. nemoralis* occur with high frequency, but *C. hortensis* shells tend to be yellow with fused bands. "The visible effect, an overall brown appearance, is very similar in both species, but the means of attaining it are different" (Clarke, 1960: 441). Clarke believes that genes for brown ground color may be less advantageous against the genetic background of *C. hortensis* than they are against that of *C. nemoralis.*

The controversy has been reasserted with regard to Cain and Currey's (1963) "area effects"—remarkably rapid shifts in morph frequencies over very small distances. These they attribute to the selective action of cryptic environmental differences, but Goodhart (1963) has emphasized chance genetic assortment in small founding stocks (see also Goodhart 1962). Recently, Clarke (1966) has proposed a selection model for the production of sharp local changes in clines which appeals neither to cryptic (i.e., unobserved) environmental discontinuities nor to the founder principle.

b) *Partula:* Crampton (1932) found no correlation between form and environment for the Partulae of Moorea and assumed that selection had little to do with establishing and maintaining the diversity among local populations. By comparing Mahalanobis distance functions constructed from Crampton's four variables (height, width, aperture height, aperture width), Bailey (1956) found that an invading subvariety is always more dissimilar to the displaced or preinhabiting subvariety than is its related non-invading subvariety; he thus concluded that selection is operating to increase the distinction of sympatric subvarieties: "The invading variety would be visualized as hybridizing with the preinhabiting variety to a limited extent. This would enable natural selection to build up mechanisms to limit further production of these (assumed) less adaptive hybrids" (Bailey, 1956: 365). There are several weaknesses in Bailey's arguments:

i) Bailey shows that selection tends to *preserve* varieties when they invade territory inhabited by others. The *origin* of races may still be attributed to the founder principle.

ii) Bailey maintains that population sizes are too large for genetic drift. This is certainly true now, but we have no idea of the size of the founding populations, the first invaders of a new valley.

iii) Crampton's traits "have not been shown to be neutral or lacking in selection pressure" (Bailey, 1956: 365). This is a straw man often constructed in such arguments: that every trait separating two groups is of adaptive significance does not necessarily imply that the difference arose by selection. Differences established by drift may be less adaptive, but if the founding population is completely isolated, the slightly more advantageous constitution of its parental population is virtually irrelevant.

Although I am myself predisposed to favor explanations giving a dominant role to selection, I find a logical flaw in the arguments of those who would cite selection as a more or less completely sufficient cause. Advocates of random effects construct their argument in this conditional form: "If the results cannot be explained by selection, then random effects must be invoked." Supporters of selection have tried to show that results can be explained by selection,[1] but this denial of the antecedent cannot falsify the statement, for the citation of a possible cause does not confirm its actual operation. I do not consider selective explanations so inherently preferable that their mere consistency with results is

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[1] For example, Cain and Currey (1963: 471): "The interaction of selective forces is complex, and seems to leave little scope for purely random effects."

sufficient to deny alternatives. Actual observations of the work of selection (visual predation studies in *Cepaea*) are more confirmatory, but these usually demonstrate the role of selection in maintaining differences among established populations; random effects may be involved in the origin of these differences.

What causes the differences in morph frequencies among local populations of subspecies in the polymorph complex of *P. cupula?* Visual predation by vertebrates seems unlikely. No native Bermudian tetrapod has been observed to eat snails, and no evidence of bird predation has ever been obtained. Smaller enemies may have been important factors in *P. cupula* mortality. Isopods, nematodes, beetle larvae, mites, land planarians, and infusorians are substantial natural pests of *Bradybaena similaris* (Komai and Emura, 1955). Physiological correlates of color conferring resistance to these enemies may have favored certain morphs. Ewers and Rose (1965) found that banded individuals of the Australian marine snail *Velacumantus australis* were less likely to harbor trematode parasites than unbanded specimens. Physiological correlates of color also confer varying resistances to physical factors of the environment. In *Cepaea*, the yellow bandless form is more resistant to high temperatures than pink and banded individuals. Guerrucci-Henrion (1966: 409) believes that most differences in morph-frequencies among populations of *Cepaea nemoralis* are tied to adaptive physiological features linked with the determinants of color. The morphs of *Bradybaena similaris* differ significantly in growth rate and in susceptibility to low temperatures (Komai and Emura, 1955).

One aspect of the temporal distribution of polymorph populations could be interpreted as favoring explanations involving random processes: the oldest populations exhibit all four morphs; geologically younger populations invariably lose at least one and as many as three color forms. A few founding individuals would not be expected to possess the genetic factors for all color forms. Moreover, since the genitalia of *Poecilozonites* suggest the possibility of self-fertilization (see Chapter 2), it is likely that many new populations begin with the genetic information of only a single individual. *Limicolaria martensiana* exhibits four genetically determined color morphs, but various forms are absent in some populations usually the rarest form in the smallest populations (Owen, 1965).

Another observation, however, is more easily explained by selection. Size at the fifth whorl is correlated with intensity of coloration as represented by the morphs; other graded physiological responses may likewise be linked with color. If random processes were responsible for the stabilization of certain morphs, the distribution of these morphs in populations possessing fewer than the complete set would not be expected to follow a definite pattern. Instead, populations with 2 or 3 morphs always possess a graded series (ab, bcd, or cd, never ac, acd, etc.). This would be expected if the stabilization of morphs is a by-product of selection for large or small size at the fifth whorl.

I am therefore caught in the paradox cited above. Observed temporal patterns are consistent with an explanation involving selection alone, but this does not disprove the possible role of random factors. I would be surprised if reduction of color variability in the few chance founders of new populations played no role in the stabilization of morph subsets in post-Walsingham populations of *P. cupula.*

VII. EVOLUTION OF THE *P. NELSONI* STOCK

A) Introduction

1. *Basic features of P. nelsoni.* The size of organisms, as Huxley has remarked, has a fascination of its own. As the sequoia of Bermudian snails, *P. nelsoni* has long at-

tracted special attention from naturalists. Lieut. Nelson, for whom the species was later named, spoke in glowing terms of "a large and delicate *Helix*" so common in Bermuda's caves that in a single instance, "upwards of thirty bushels were recovered without any earth among them" (Nelson, 1840, quoted in Verrill, 1905: 160). Pilsbry, too, noted its "remarkably large" size (1888: 290).

The type specimen of *P. cupula multispira*, largest known individual of its species, measures 34.2 mm in height plus width, while a *P. bermudensis zonatus* from Charles Island reaches a size of 42.1 mm. In contrast, the largest *P. nelsoni* (Shore Hills Soil, Main Fissure, Government Quarry) measures 77.6 mm and specimens exceeding 70 mm are common in many localities.

The other distinguishing features of *P. nelsoni* are all related to its size. In most samples, mean size of the protoconch exceeds that of other taxa. Since the protoconch fills the egg and since larger snails tend to lay larger eggs (Rensch, 1932), this observation should entail no surprise. The larger protoconch implies larger size at subsequent whorls but this differential is not sufficient to account for the size of *P. nelsoni*. At the fifth whorl, the largest *P. nelsoni* exceeds the largest five whorled *P. bermudensis* by only 8 per cent. Most of the difference in size is related to the greater whorl number of *P. nelsoni*. An 8-whorled specimen is not uncommon, while *P. cupula* and *P. bermudensis* (with the exception of *P. cupula multispira*) rarely exceed six whorls. The mean differential growth ratio of *P. nelsoni* is less than 2.0 in 15 of 21 samples; in *P. cupula* and *P. bermudensis* such low values are characteristic only of *P. cupula triangularis* and some paedomorphic samples of *P. bermudensis*. The higher the differential growth ratio, the faster the increase of height vs. width in ontogeny. If not counteracted by low initial form index or unusually large early whorls, high differential growth ratios limit final size by rapid production of a disadvantageously high spire (Gould, 1966a). The moderately large early whorls and low differential growth ratios of *P. nelsoni* allow this species to maintain reasonable proportions to sizes at which *P. cupula* and *P. bermudensis* would possess a spire too high for efficient locomotion (Gould, 1966a: 1135).

2. *The biospecies in paleontology.* To many paleontologists, the infusion of population thinking has meant only that the normal curve should replace the holotype as a reference standard for the definition of species. The winnowing of a few biologically meaningful taxa from masses of names erected for individual variants has been the most satisfying result of this replacement. Indeed, in most paleontological studies, application of the biological species concept cannot progress much beyond this morphological criterion of species recognition. And yet, the biospecies is primarily an ecologic notion in that the criteria used for inferring the genetic relationships that lie at its core are not those of morphology, but rather those of habitat, behavior, and geographic distribution.

Faced with the dilemma that nonmorphological information is rarely provided by fossils, must the paleontologist abandon the biospecies as inapplicable to his studies (as Weller, 1961, has proposed)? My qualified "no" is based on two arguments:

1. A general statement: Unless a theoretical concept is thoroughly non-operational, in which case it may be reasonably abandoned as meaningless, practical difficulties in application do not demand rejection.

2. A strategy: While admitting that most fossil occurrences do not provide the nonmorphological information needed to define a biospecies properly, I would argue that a paleontologist particularly interested in the study of species ought to seek those

favorable cases in which such information is available.

The Bermudian Pleistocene is a favorable case. Within a span of time far shorter than the margin of error in most geologic correlations, 10 island-wide stratigraphic units have been established. Some, the Harrington unindurated zone in particular, are of such limited temporal extent that geographic distributions for a given instant may reasonably be inferred from the fossils found within them.

Given this degree of resolution, the nonmorphological information crucial to many taxonomic decisions becomes available. In particular, we now have criteria for determining whether two samples sufficiently distinct for taxonomic separation are subspecies or species. This is a decision that simply cannot be made without nonmorphological information. The standard paleontological use of subspecies to express morphological differences smaller than those required of species, does not automatically provide taxa in accord with the biological definition of this rank;[1] for we know that one of a pair of species is often more similar to the other in size and shape than it is to the subspecies of its own polytypic taxon. Since species and subspecies are defined by interbreeding relationships that can often be inferred from geographic distribution, we have the following criteria to supplement our morphological base:

1. Non-interbreeding sympatric populations are species. (In fossils: biomodality not due to sexual dimorphism, age, etc., among specimens from a single locality not coagulated by *post mortem* transport.)

2. Potentially interbreeding allopatric local populations are subspecies. (A group of fossil samples, each of distinct morphology and each occupying a discrete, nonoverlapping portion of the species' total geographic range at a given moment in time.)

B) History of the P. nelsoni Stock

1. *Previous work and new recommendations.* The existing subspecific classification of *P. nelsoni* is a compendium of shapes established by typological systematists before the geology of Bermuda had been unravelled. Five names are available:

1. *P. nelsoni nelsoni* (Bland) 1875. "Normal" samples having a weakly developed callus and adult width/height ratio of about 1.5 to 1.7 have been referred to the nominate subspecies. (Pl. 2, fig. 3).

2. *P. nelsoni discoides* Gulick, 1904. Gulick (1904: 416) suggested the name *discoides* "merely as a convenient term" for low-spired but otherwise "normal" specimens. Verrill (1905) and all subsequent authors have treated this suggestion as a formal trinomial (Pl. 2, fig. 1 is the holotype).

3. *P. nelsoni conoides* Verrill, 1905. Although he acknowledged that "this variety passes into the others by all intermediate gradations," Verrill (1905: 163) gave formal recognition to "the high-spired or conical form of this species, in which the height is from two-thirds to nine-tenths the diameter of the shell, or sometimes equal to it" (Pl. 2, fig. 4 is a topotype). Verrill (1905) describes the type locality of this form as "Western shore of Castle Harbor in a mass of red-clay and stalagmite." Haycock's label (collection at the Bermuda Museum) for his *P. n. conoides* specimens lists their source as "Gulick's locality 806, the types for Verrill's *P. conoides.*" Now Gulick's 806 is also the type locality of *P. n. discoides* and, indeed, Gulick listed the extreme shapes for shells of this locality as Alt. 34, Diam. 34 mm (a typical *P. n. conoides*) and Alt. 19.5, Diam. 39 mm (the type specimen of *P. n. discoides*); Gulick designated only the low-spired individuals as *P. n. discoides.* This locality has been

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[1] I am not suggesting that this practice be abandoned, but merely pointing out that it represents a use of the Linnaean system more for the cataloguing of morphological diversity than for the understanding of biological relationships.

obliterated by progress and now underlies a sand trap of the Castle Harbour Hotel golf course.

The snails assigned to this subspecies were found in fissures of a Walsingham cave filled with Shore Hills Soil. We do not know whether the two names represent the artificial division of a single variable sample or the fossil remains of two different fissures. Despite the tremendous diversity of form among samples, I have never made a collection in which the range of within-sample variability was even nearly sufficient to encompass these two extremes in spire height. On the other hand, the caves and quarries of this area are studded with soil-filled fissures. The fissures were filled at different times within the Shore Hills, and each of several fissures within a locality may contain a distinctive fossil sample. I suspect, therefore, that the names *P. n. conoides* and *P. n. discoides* were applied to morphologically coherent samples from different fissures of a single locality.

4. "*P. nelsoni gulickiana.*" Though it never appeared in print, Pilsbry intended to establish this taxon for a sample from Locality P3, for he wrote the following Latin note: "n. subsp.: P. n. callosus Gulicki prop., sed major carina validior et color diff. P. nelsoni gulickiana Pils." [Close to Gulick's *P. n. callosus*, but stronger carina . . .] The color pattern of these shells, $1^{f}23$, is the usual one for *P. n. nelsoni* (to which this sample is most closely related despite Pilsbry's statement); *P. n. callosus* (discussed below) is 023. (Pl. 2, fig. 6 is the specimen which would have been made the type of this taxon.)

5. *P. nelsoni callosus* Gulick, 1904. The holotype (Pl. 3, fig. 2), from "Benj. Trott's sand pit, Tuckerstown," represents a group of samples distinguished from other forms of the species by their smaller size, large number of whorls, and prominent parietal callus.

The use of a classification rooted in outdated principles chains us to those principles. My goal in reassessing the classification of *P. nelsoni* is not to establish a "better" order (if such an adjective is even appropriate to human contrivances), but to arrange taxa in accord with modern principles, thereby providing a vocabulary that allows these principles to be discussed. In seeking taxa which correspond to biological populations, two aspects of previous methodologies seem especially obstructive. First the subjective appraisal of morphology based on one or just a few characters should be replaced by a more objective evaluation of many variables and their interrelations. Especially suspect is the subspecific sequence *discoides-nelsoni-conoides*, based as it is solely on the variable character of spire height. Measurement of many characters with subsequent simplification and representation by factor analysis was successful for *P. cupula* and will be used here. Secondly, the naming of mere shapes must be extended to a study of the geographic and temporal distribution of such shapes.

When the second recommendation is followed, some regularities are noted immediately. In particular, the two major lithologies, red soils and eolianites, contain distinct aspects of the total fauna: *P. nelsoni callosus* is confined to eolianites (a persuasive argument for its validity), the other four named taxa to red soils.

2. *Distribution and variation of the P. nelsoni stock in red soils.* Sayles (1931) and Bretz (1960) took as their main paleontological guide to Bermudian stratigraphy the supposed absence of *P. nelsoni* above the Harrington soil. This species is, however, reasonably common in Pembroke dunes and has now been found (by L. S. Land and myself) in the St. George's at adjacent localities 18 and 68; its range, as known today is Shore Hills to St. George's.

The outstanding feature of *P. nelsoni* is its diversity. From sample to sample, differences in basic shape and shell thickness occur in combination with a great variety of themes on the color pattern 123.[1] Yet variability within samples is not nearly so great (color characters are particularly diagnostic). As in *P. cupula*, almost every sample of *P. nelsoni* is sufficiently unique to allow the unambiguous assignment of a single well-preserved shell to its proper sample. So marked is this distinction that each of several Shore Hills fissure fills of some Bermudian quarries may contain its particular assemblage. Gulick (1904) was sufficiently modern in approach to avoid mixing snails of the same species from different localities, but he lumped fissures within localities, thereby obscuring important patterns of infraspecific variation. In Government Quarry (locality 5), for example, three of the numerous fissures contain large numbers of *P. nelsoni* (while a fourth, dubbed "the graveyard" by local quarrymen, is a massive coquina of *P. bermudensis zonatus*). The "Main Fissure" on the south wall contains large, rather thick shelled, narrowly umbilicate specimens with strong 123 coloration and an angulate aperture with sharp carina. Snails of the "Bird Fissure" (type locality of the crane *Baeopteryx latipes*) are large, thin shelled, and widely umbilicate, with strong 123 coloration and a rounded aperture (Pl. 2, fig. 7). The "Coquina Fissure" on the west wall is filled with small, low-spired, and delicate *P. nelsoni* whose weak coloration is evident in the narrowness of bands 2 and 3 and the persistence of flames in the band 1 position.

Morphological relationships among 24 samples (each represented by the standardized means of 24 variables)[2] are shown in Figure 14, a plot on varimax axes 1 and 2 of a three axis Q-mode solution; the three axes account for 94.0 per cent of the total information of all samples, while the first two encompass 88.8 per cent. Numbers 1 through 11 represent red-soil *P. nelsoni* samples assignable, under criteria previously used, to the subspecies *P. n. nelsoni* and *P. n. discoides*. Samples with relatively wide shells project strongly on the first axis and weakly on the second; the diagonal array of *P. nelsoni* reflects an increase in relative height moving from upper left (number 6 is the type sample of *P. n. discoides*) towards lower right. Samples are evenly spaced along the array and do not cluster into discrete morphological groups. Moreover, samples on the "*discoides*" end of the array are distributed erratically in space and time. The coincidence of morphological clusters with unique spatio-temporal distributions, the criterion by which subspecies were defined in *P. cupula*, does not occur here. Of the four discoides-like samples, number 6 (type *discoides*) is widely separated from its Shore Hills geographic neighbors (numbers 1–5); 8 and 9 are from the opposite western end of Bermuda and 10 (Pl. 2, fig. 2) is one of the two St. George's samples (the other being number 11, most "intermediate" of the red-soil *P. nelsoni*). We have either a polytopic subspecies or

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[1] In no other taxon of *Poecilozonites* is there as much infraspecific variation in band onsets and widths within a single pattern. Among red soil samples, only Ireland Island and Cambridge Beaches (localities 65 and 97) do not exhibit the 123 pattern; these lack the upper band and are coded 023. This is particularly intriguing because these samples are the only red-soil *P. nelsoni* from western Bermuda. *P. bermudensis*, discussed in the next chapter, has the same geographic distribution of color: all eastern samples are 123; all western, 023. I do not have enough *P. nelsoni* samples to tell whether the distributions are exactly alike, nor can I pick a preferred hypothesis among the several possibilities of sheer coincidence, similar selective pressures in isolated environments, genetic interchange between the two species, etc.

[2] Non-standarized variables are considered at 40 mm height plus width. Two important samples could not be included in this plot because the sample range in size was insufficient to construct meaningful regressions for predicting values of non-standardized variables at 40 mm. As paratype material belonging to other museums, the shells of these samples (type localities of *P. n. conoides* and "*P. n. gulickiana*"), all of large size, could not be broken back to produce the required size range.

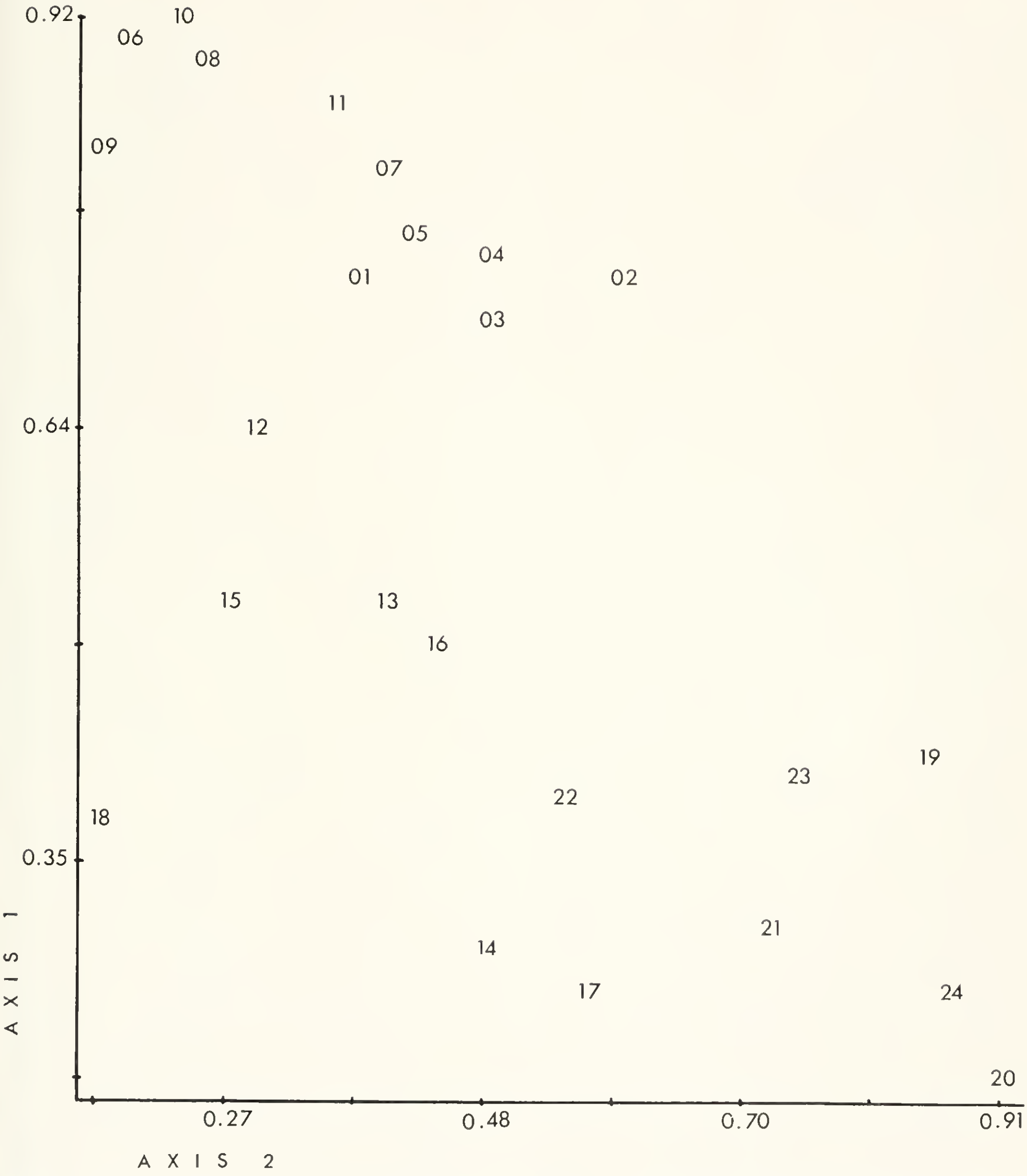

Figure 14. Plot on varimax axes of all samples of the *P. nelsoni* stock. *P.n. nelsoni* (nos. 1–11), *P.n. callosus* (nos. 12–18), *P.s. superior* (nos. 19–20), and *P.s. arenicolus* (nos. 21–24).

a group of samples which have acquired independently a low spire and its set of mechanical consequences (wide umbilicus, relatively wide aperture, etc.). As a character, spire height is so eminently labile that the second alternative seems preferable. The type sample of *P. n. conoides*, likewise, is little more than the highest spired of a morphologically intergrading series of local populations (Pl. 2, figs. 1–5).

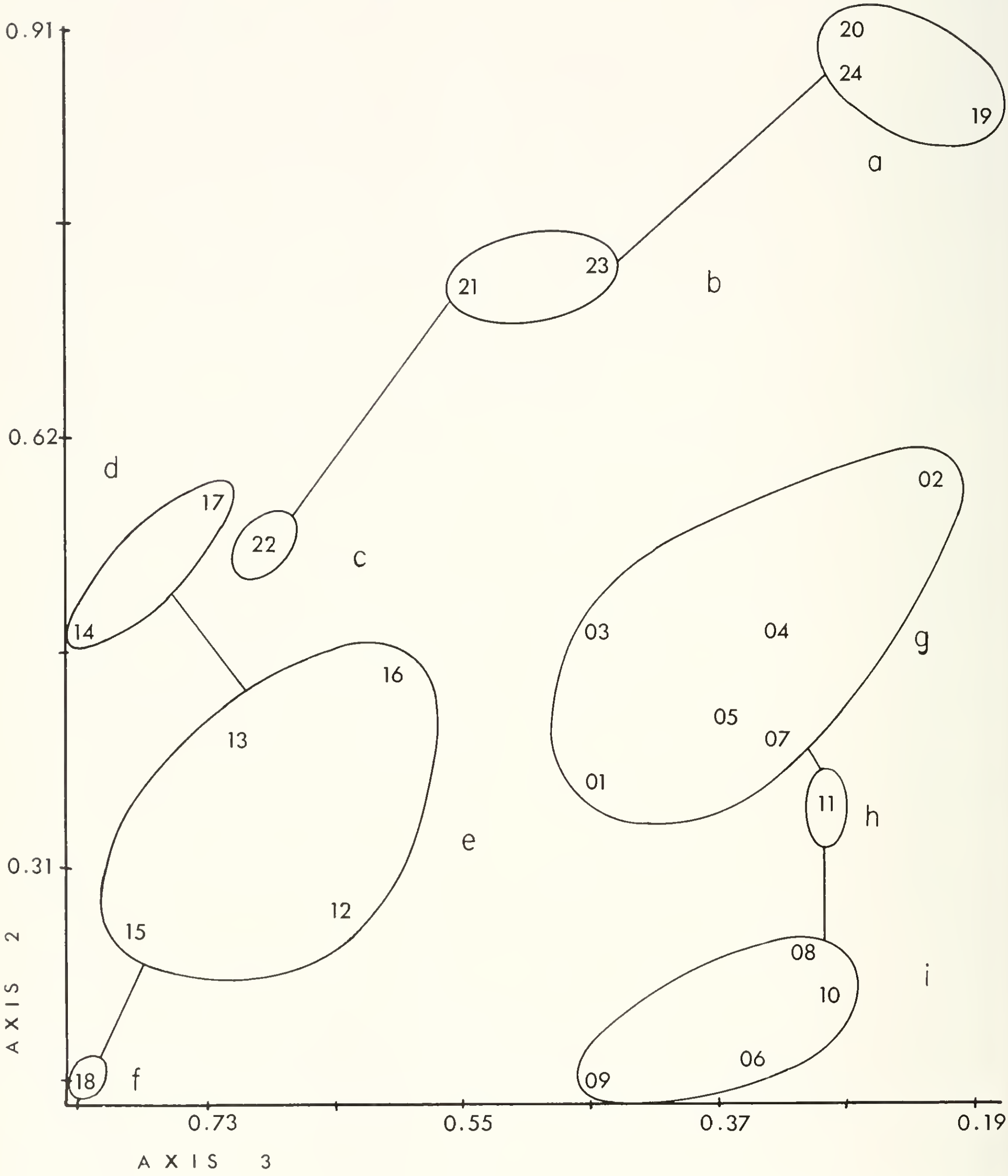

Figure 15. Plot on varimax axes of all samples of the *P. nelsoni* stock. Numbers as in Figure 14. Letters as follows: A, high-spired *P. superior*; B, intermediate *P. superior*; C, low-spired *P. superior*; D, high-spired *P. nelsoni callosus*; E, typical *P. nelsoni callosus*; F, low-spired *P. nelsoni callosus*; G, typical *P. nelsoni nelsoni*; H, intermediate *P. nelsoni nelsoni*; I, low-spired *P. nelsoni nelsoni*.

Finally, "*P. n. gulickiana*" presents no special singularities; its callus does surpass the other red-soil *P. nelsoni* in thickness, but the sharpness of its carina is exceeded by the Ireland Island specimens, the angularity of its aperture by Government Quarry Main Fissure shells, and the weakness of its 1^f23 coloration by the type *discoides* and Government Quarry Coquina Fissure samples. To establish subspecies of red-soil *P. nelsoni*, we would need both morphologically discrete sample groups and a geographic distribution linking distinct shapes to non-overlapping geographic areas. Neither of these conditions is fulfilled, and I propose that *P. n. discoides*, *P. n. conoides*, and *P. n. gulickiana* be synonymized with Bland's *P. n. nelsoni*.

This, however, is not the complete story of red-soil samples. Found with normal *P. nelsoni* shells in the Bird Fissure of Government Quarry is a group of specimens whose clear morphological distinction is beyond doubt. (The bimodality for size at the fifth whorl is shown in Figure 16.) Although resembling *P. nelsoni* more than any other taxon of the genus, these specimens share a large set of non-redundant characters unknown in red-soil *P. nelsoni* samples—small final size and small size at a whorl, small protoconch, relatively high spire, high differential growth ratio, and 123 coloration with sharp band margins and no tendency for band fusion. This sample, number 20 of Figures 14–15, projects very weakly on the first axis and most strongly upon the second, which serves as a reference for small, high-spired shells. Of the various causes of bimodality at a locality, sex can be excluded for these hermaphrodites. Age cannot be invoked, because the two groups are distinct not only at their final sizes but also at comparable sizes and whorl numbers (Figs. 14–15, of course, treat all samples at a standardized size). *Post mortem* transport seems unlikely for these exquisitely preserved specimens. Moreover, I have never seen evidence of extensive mixing in any of the numerous Shore Hills fissure fills of this area. Several species may occur in the fill, but the shells of any one always possess the morphological coherence of a single local population. We seem, indeed, to be dealing here with two distinct sympatric taxa, i. e. with two species. This conclusion is affirmed by two additional discoveries. By the summer of 1967, Bird Fissure had been blasted away and a new one (or branch of Bird Fissure) opened nearby. The new fauna is identical to that of Bird Fissure—the cahow *Pteroderma cahow*, the distinctive crane *Baeopteryx latipes*, the widely umbilicate *P. nelsoni*, and high spired shells of the new species. I measured the protoconch width of all snails; those of *P. nelsoni* and the new species are distinct at any commonly used significance level ($t = 10.69$ at 56 degrees of freedom). Moreover, a fissure on the south wall of nearby Wilkinson's Quarry locality 34) contains fragments of *P. nelsoni*, several of the small high-spired snails (number 19 of Figs. 14–15) and, again, the crane *B. latipes*. These, in fact, are the only known occurrences of *B. latipes*. The fissure fills of the Walsingham district span a glacial epoch, but individual fissures probably filled rather quickly. In these three fissures, we seem to pick up traces of a unified fauna that inhabited the area for a short duration of the total span. At this time, two large species of *Poecilozonites* lived together in the area. For the

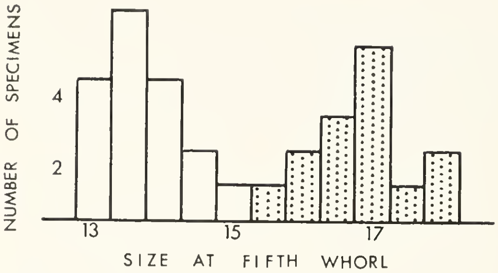

Figure 16. Histogram of size at fifth whorl for all *P.* (*Poecilozonites*) found in Bird Fissure, Government Quarry. Dotted specimens are *P.n. nelsoni*, blank *P.s. superior.*

smaller, higher-spired form, I propose the name *Poecilozonites superior* in reference to the elevated spire. (The two species of Bird Fissure are shown in Pl. 2, figs. 7 and 8; formal descriptions will be found in the first appendix.)

In conclusion, two species of large *Poecilozonites* lived in Shore Hills red soils (*P. superior* is unknown from the St. George's). All names previously proposed for red-soil *P. nelsoni* samples are synonymous with *P. n. nelsoni* itself. Non-morphological data were needed to eliminate these superfluous subspecies, for shells shaped appropriately for inclusion under any one of them do not possess the geographic distribution required of biological subspecies. Likewise, sympatric occurrence of *P. nelsoni* and *P. superior* led to their definition as separate species. Thus, both non-morphological criteria of page 460 were usd to establish a classification sufficiently consistent with population structure to permit, or at least not to hamper, an evolutionary interpretation of these taxa.

3. *The P. nelsoni stock in eolianites.* Shells from the *P. n. callosus* type locality, a sand pit of presumed Harrington-Pembroke age, are similar to *P. n. nelsoni* in general shape (Pl. 3, fig. 2), but differ from all red-soil samples in several ways: they are smaller in maximum size and smaller at standardized sizes (from protoconch width to size at the seventh whorl); the shell is thickened (leading to a restricted umbilicus) with a strong callus on the parietal portion of the aperture; the color pattern is, invariably, 023. A number of other Harrington-Pembroke samples share this set of features (numbers 12–18 of figs. 14–15), though each has distinguishing characters that render it unique: the North Shore Road sample (No. 12) is larger-at-a-whorl than all others and therefore projects most strongly upon axis 1, which serves as a reference for large, red-soil *P. nelsoni.* The samples from Sayles's type locality of the Harrington Formation[1] (numbers 14 and 17, and Pl. 3, fig. 1) surpass the others in relative height and project strongly upon axis 2 (the reference for high-spired Shore-Hills *P. superior*). The low-spired St. David's Island shells (number 18 and Pl. 3, fig. 3) are remarkably thick and heavily callused (and have a *wide* umbilicus despite the usual negative correlation of shell thickness and umbilical width). Thus, the validity of Gulick's *P. nelsoni callosus* is affirmed, not from its morphological uniqueness alone, but because it, unlike the rejected subspecies of Gulick, Verrill and Pilsbry, occupies a distinct spatiotemporal segment of the species range.

The Harrington-Pembroke formations contain yet another group of samples. These (numbers 21–24 of Figs. 14–15) are high spired, lack a strong callus (despite shell thickness equal to that of *P. n. callosus*) and, especially, exhibit color patterns 103 or 12^n3 (band 2 is always well developed in *P. n. callosus*, band 1 always absent). Although they have never been found together in the same outcrop, the range of these samples is coextensive with that of *P. n. callosus.* This implication of sympatry and tendency toward high spires suggests that these samples are a subspecies of *P. superior,* here named *P. superior arenicolus* in reference to its dune habitat (Pl. 3, figs. 4 and 5).

When all samples of the *P. nelsoni* stock are considered, we can delimit three major morphologies: the large, thinly callused, relatively low-spired *P. n. nelsoni;* the small, thickly callused, relatively low-spired

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[1] I collected number 14 at Sayles type Harrington, but found number 17 in the Sayles collection at Antioch College, labelled simply "South Shore Harrington Sound"—an area including the type Harrington but not excluding other exposures. That the two are drawn from the same local population (and probably come from the same exposure) is indicated by their close similarity as measured by all variables. They appear closely together on all varimax plots.

P. n. callosus; and the small, thinly callused, relatively high-spired *P. superior superior* and *P. s. arenicolus*. The first three varimax axes (94.0 per cent of the total information) encompass these three trends in form. *P. n. nelsoni* samples sort with the first axis, the largest and lowest spired samples doing so most strongly. The second axis is a reference for *P. superior;* the highest projection on this axis is that of the smallest and highest-spired sample, the Bird Fissure *P. s. superior.* Grouping with the third axis (Fig. 15) are shells of *P. n. callosus:* the St. David's Island sample, smallest, lowest-spired, and most strongly callused of *P. n. callosus* samples, projects most strongly on this axis. When each sample is grouped with the oblique axis upon which it projects most strongly (Table 10), virtually complete discrimination of the taxa is obtained. Of 24 samples, only one is misallocated; the Trunk Island sample of *P. s. arenicolus* (number 22 of Figs. 14 and 15), lowest spired of its species, groups with the *P. n. callosus* samples.

TABLE 10. OBLIQUE PROJECTION MATRIX FOR ALL SAMPLES OF THE *P. NELSONI* COMPLEX. The following identifying information is given for each sample: trivial name of the subspecies, locality number and age (SH = Shore Hills, HP = Harrington-Pembroke, SC = St. George's).

Sample			Axis 1	Axis 2	Axis 3
nelsoni	18	SG	1.000	0.000	0.000
nelsoni	65	SH	0.969	0.050	0.033
nelsoni	P2	SH	0.946	−0.068	0.114
nelsoni	68	SG	0.921	0.199	−0.018
nelsoni	30	SH	0.853	0.263	0.008
nelsoni	5B	SH	0.796	0.506	−0.172
nelsoni	97	SH	0.785	−0.083	0.312
nelsoni	89	SH	0.779	0.366	0.004
nelsoni	P9	SH	0.770	0.283	0.094
nelsoni	5M	SH	0.682	0.244	0.234
nelsoni	5C	SH	0.599	0.332	0.246
superior	5B	SH	0.000	1.000	0.000
arenicolus	?	HP	0.090	0.970	−0.019
superior	34	SH	0.348	0.888	−0.173
arenicolus	11	HP	0.200	0.737	0.237
arenicolus	63	HP	0.007	0.730	0.422
callosus	84	HP	0.000	0.000	1.000
callosus	45	HP	−0.137	0.406	0.896
callosus	86	HP	0.182	0.077	0.861
callosus	?45	HP	−0.149	0.546	0.766
callosus	30	HP	0.242	0.277	0.678
arenicolus	100	HP	0.055	0.474	0.657
callosus	95	HP	0.462	0.139	0.559
callosus	P8	HP	0.270	0.382	0.518

Of course, each taxon must be seen not as if glued to a set of distinctive characters, but rather as operating in a reaction range that does not include the total form spectrum of the entire stock. Overlap will occur where the ranges intersect. Were it not for differences in color and callus, the lowest-spired *P. s. arenicolus* (number 22) might not be distinguished from the highest-spired sample of *P. n. callosus* (numbers 14 and 17). One genetic difference between *P. nelsoni* and *P. superior* lies, presumably, in the ability of the former species to produce a callus. This potential is translated to morphology in eolianite environments (carbonate dunes), where lime sufficient for its production is available. Samples of the two species in this environment can be distinguished thereby. In calcium-poor red soils, the potential remains that alone and, in the further absence of firm color distinctions, allocation of a sample to its proper species is difficult in certain cases. I have found no way to tell, for example, whether the single magnificent specimen from a small fissure on Harrington Sound Road (Pl. 2, fig. 5) is an exceptionally high-spired *P. n. nelsoni* or a large *P. s. superior.*

C) Mode and Significance of Temporal Changes in Morphology

The most satisfying aspect of observed morphological differences between red-soil and eolianite samples is the availability of a reasonable adaptive explanation. Such explanation is particularly welcome in pulmonates, since it has been claimed so often that patterns in diversity bear no relationship to environment in this group.[1] The three features which distinguish virtually all eolianite samples from all red-soil shells are the smaller size (absolutely and at a whorl), the thicker shell, and the weaker coloration (023, 103 or 12^n3 with a tendency for narrower bands of lighter color—this lightness, however, may be a preservation artifact—compared with the generally wide and dark bands of the red-soil 123 pattern). (The fourth feature, a narrower umbilicus, is a consequence of restriction by shell thickening in *P. n. callosus* or by thickening and increasing relative height in *P. s. arenicolus.*)

The relationship of size and environment is obscure, though Rensch (1932) has suggested that the absence of dry spells produces larger shells by reducing the percentage of lifetime spent in estivation. Bermuda was wetter during glacial (red-soil) periods (see Chapter 9). The weaker coloration can be explained in two ways. Rensch (1932) found a strong positive correlation between increasing mean intensity of solar illumination and weaker coloration; the whiter the outer shell layer, the more reflective of light. The white dunes must have received more illumination than thickly vegetated soils of the wetter glacial periods. Alternately, the weak coloration of eolianite snails may have been cryptic. I suspect that the white dunes were sparsely vegetated, as are the modern dunes of Elbow Beach and Tuckerstown. The red soils were not only deeply colored in themselves, but also mantled in vegetation if today's situation is representative (Bermuda's agriculture is centered on exposures of the fossil red soils).

Differences in shell thickness are most easily explained. It has been shown again and again (see Chapter 9) that land snails extract lime for their shells from the rocks upon which they live (viz. the abundance of pulmonates on many limestone outcrops). Normally thick-shelled species produce paper thin shells (if they survive at all) when deprived of calcium carbonate (Oldham, 1934, Rensch, 1932). The eolianites are all carbonate, while $CaCO_3$ constitutes less than 2 per cent of some red soils (Ruhe, et al., 1961). Shell thickening and loss of color are attained in two different ways in two independent taxa. Such multiple solutions may be taken to indicate the adaptive necessity of these modifications.

One final question must be posed: Did the eolianite subspecies evolve directly from Shore Hills progenitors (and then back again to produce the St. George's *P. n. nelsoni*—see Henningsmoen, 1964, on zigzag evolution), or did two subspecies of each species persist in different areas and environments from, at least, Shore Hills through Pembroke time. As is usual in paleontology, the literal interpretation of zigzag evolution is less likely. The two subspecies of each species are distinguished by a large set of characters, not all of which can be presently seen as subject to precise and necessary expression in given environments. Thus, we would expect a St. George's derivate of *P. n. callosus* to reacquire the thin shell and strong coloration of the Shore Hills *P. n. nelsoni,* but we would not anticipate so precise a return to previous morphologies. This, however, is not the strongest argument.

Bermudian stratigraphy is a complex of facies, not a layer cake. Throughout the Pleistocene, dunes formed at the periphery of the islands and became cemented before they could migrate inland (Bretz, 1960; Land, Mackenzie, and Gould, 1967); red soils formed in sheltered central parts. During glacial times, the island periphery stood several miles out and a few hundred

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[1] This debate is discussed in Chapter 9 which treats, in much greater detail, the whole question of climate and evolution in land snails. This chapter should be consulted for the documentation of statements cited here without evidence, e.g. of the contention that shell thickness is related to the availability of calcium carbonate in the environment.

feet below present sea level. Of dunes formed in glacial times, only North Rock, a small pinnacle ten miles off Bermuda's north shore, remains awash. A vertical sequence of red soil-eolianite-red soil therefore reflects the migration of environments in response to shifts in sea level. The corresponding faunal sequence, *P. n. nelsoni-P. n. callosus-P. n. nelsoni* need not represent evolution *in situ* but is, more likely, the fragmentary record at one point in space of the fact that two subspecies, each tied to a particular environment (hence to a particular geographic domain), lived through the time of the entire sedimentary sequence. (This possibility, by the way, was the basis of Newell's argument that the "chronological subspecies" is not necessarily an artifact of convenience having no relation to its biological counterpart of local races occupying a geographic subsection of the species range—Newell, 1947). The first possibility, zigzag evolution, carries the implication that a given environment elicits a definite morphological response (which may be phenotypic only) in all cases. The second, that of well-defined, long-ranging subspecies, suggests that each subspecies is a distinct genetic entity (still capable of interbreeding with others, of course). Hence, even if an occasional local population survives in the "alien" environment, it will not alter in form to identity with the usual subspecies of that environment, but will retain enough of its features to be recognizable. I find it a most convincing test of this second possibility that such local populations have twice been found in Bermuda:

1. In an eolianite of Harrington age exposed on South Shore Road at Saucos Hill (locality 64): a few specimens clearly assignable to *P. n. nelsoni* (large protoconch, strong 123 coloration—see matrix of means in appendix). The two preserved calluses are thicker than those of any other *P. n. nelsoni.* Shell thickness, if a simple function of the availability of lime, will alter in immediate phenotypic response to this factor.

2. In the Shore Hills soil at Ferry Road, north of the Biostation locality 11: four shells which, in their high spire and 12^n3 coloration with sharp band margins, possess the distinguishing characters of *P. s. arenicolus.* These are, however, thin-shelled, demonstrating once again the response of shell thickness to environment of deposition.

I conclude that the *P. nelsoni* stock, as known today, consists of two closely-related species; each of these is, in turn, divisible into two subspecies, one adapted to red soils, the other to eolianites. These two environments persisted throughout the Bermudian Pleistocene, migrating back and forth across the platform in response to fluctuating sea levels of the ice age. The subspecies migrated with the environments and a vertical sequence, though giving the appearance of zigzag evolution, merely reflects the view of a static observer who spent the Pleistocene watching the march of environments at his single station.

VIII. PHYLETIC BRANCHING IN THE *P. BERMUDENSIS ZONATUS* STOCK

A) Introduction

Of the four species of *P.* (*Poecilozonites*), *P. bermudensis* is most abundant by far as a fossil; shells are plentiful and well preserved in all post-Belmont formations. In addition, *P. bermudensis bermudensis* is the only living representative of the subgenus. The high precision of temporal and geographic control and the existence of a living form combine to make this species a particularly favorable object of evolutionary investigation. During the last 300,000 years, the central stock of the species, *P. bermudensis zonatus* Verrill 1902, has branched at least four times and has itself undergone fluctuating alterations of morphology that correlate with ice age climatic oscillations. Illustrated here are the two major evolutionary events of phylogeny: speciation or the multiplication of lineages and phyletic evolution or the transformation of lineages. In our microcosm, branches may not reach the specific level of distinction, and patterns of transformation may involve phenotypic modification with little genetic basis; yet the two modes are illustrated, even if in miniature. Branching of the *P. bermudensis zonatus* stock will be considered in this chapter, its phyletic transformations in the next.

Diversity of form and color among samples of *P. bermudensis* is far less pronounced than in *P. cupula*. Whereas a single well-preserved *P. cupula* shell can be identified unambiguously as belonging to one of its 13 local populations, local distinction of *P. bermudensis* is not nearly so strong; if given a single *P. bermudensis zonatus* shell, I can distinguish only between Shore Hills and later specimens and between eastern and western Bermuda. An interesting question, and one which will probably never be answered, concerns the cause of this difference in variability. Is it a taxonomic artifact? (Are the *P. cupula* subspecies really species? Is *P. bermudensis* merely a spectacularly successful side branch of the *P. cupula* stock, ranking with the *P. cupula* subspecies in genetic distinctness but given specific status because of its abundance?). Or does it reflect something more fundamental about the genetic background and habitat preferences of *P. bermudensis*?

The lowered variability of form is matched by the stability of color pattern. Only two color types (and their extensive sets of subtypes) are known in *P. bermudensis*, but the geographic distribution of these types is a fundamental datum. East of a line passing through Devonshire Marsh on the north (locality P7) and Cox's Bay (just west of locality 47) on the south, all fossil *P. bermudensis* samples exhibit band pattern 123; 023 occurs west of this line (Pl. 1, figs. 6–7). The margins of band 2 are sharp in the western forms, diffuse in eastern samples. With the exception of a single intermediate sample found by Haycock in Devonshire Marsh,[1] the distinction is as clear near the area of potential contact as at opposite ends of the island. I assume that genetic exchange between eastern and western snails was eliminated or greatly curtailed during the whole Shore Hills-Southampton interval and that *P. bermudensis zonatus* was evolving as two parallel stocks during that time. At some time after the end of Southampton deposition, *P. bermudensis zonatus* became extinct. Its primary range on the main island was quickly repopulated by *P. bermudensis bermudensis*, which had been evolving in isolation on St. George's Island since St. George's time;[2] the color pattern of all modern snails is therefore 123.

Another variation in color pattern is unique to *P. bermudensis*. In all post-Shore Hills samples of *P. bermudensis zonatus* from eastern Bermuda, a number of large shells (from 5 per cent to 80 per cent of the total collection) develop apparently normal bands, which are replaced during ontogeny by diffuse lines of color at the previous band peripheries (Pl. 5, fig. 5). The time of onset of this phenomenon, which I shall call "faded," varies but

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[1] Haycock collection, Bermuda Museum. I cannot exclude the possibility that this sample is mixed or mislabelled. The locality is now a garbage dump.

[2] This extinction, completely undocumented in the preserved record, is itself one of the most fascinating events in the history of *P. bermudensis*. Since it occurred after the latest deposition of Southampton dunes, the extinction is a very recent event, probably attributable to human disruption of the native biota. Isolated on St. George's Island, *P. bermudensis bermudensis* survived the plagues of rats, pigs, and snails that ravaged Bermuda during the early settlements (see Chapter 2) and later repopulated the whole island complex. That a few hundred years is adequate time for such a colonization (especially with the aid of human ferrying) is indicated by the work of Crampton (1916, 1925, 1932) on rapid migrations in *Partula*.

usually occurs between the fourth and fifth whorl. In samples from western Bermuda, the "faded" characteristic is either absent or present at low frequency (invariably less than 10 per cent).

B) The Branching Occurs by Paedomorphosis

The exception to the statement that *P. bermudensis* displays little diversity is provided by a group of samples which share common attributes not occurring in *P. bermudensis zonatus.* These samples occur in four discontinuous segments of the space-time framework:[1]

1. In the Shore Hills Soil exposed in caves north of Tom Moore's Tavern (locality 53), *P. b. fasolti* new subsp. (Pl. 4, fig. 3).
2. In the Harrington Formation at two localities on the southern tip of Ireland Island (locality 10), *P. b. siegmundi* new subsp. (Pl. 4, fig. 4).
3. In the Harrington and lowest Pembroke Formations at Rocky Bay (locality 44), *P. b. sieglindae* new subsp. (Pl. 4, fig. 5).
4. In the St. George's and Southampton Formations on St. George's Island, spreading to the main island after the extinction of *P. bermudensis zonatus* in recent time (localities 11, 12, 15, 16, 19, 21, 24, 27 for St. George's and Southampton fossils and 78, 79, 80, 81, 82, 83, 88 for living populations), *P. b. bermudensis* (Pfeiffer) (Pl. 5, fig. 6).

These samples are distinct from *P. bermudensis zonatus* in the following ways (non-standardized measures considered at height + width = 30 mm in all subspecies; see matrix of means, Appendix 3, for numerical comparisons and Pl. 4 for photographs):

1. Color is considerably less intense. This effect is most pronounced in *P. b. fasolti* and St. George's-Southampton samples of *P. b. bermudensis.* In shells of these populations, flames are invariably present in band positions 1 and 2; even band 3, which always forms by the third whorl in *P. b. zonatus,* may be undeveloped, its area occupied by closely spaced flames.
2. The shell is relatively much thinner.
3. The parietal callus is completely absent (*P. b. fasolti, P. b. bermudensis*) or very weakly developed (*P. b. siegmundi, P. b. sieglindae*).
4. The spire is relatively lower; a larger percentage of the total height is accounted for by apertural height.
5. The shell is relatively wider.
6. The differential growth ratio is lower.
7. The aperture is relatively wider.
8. The umbilicus is wider.
9. The cross-sectional profile of the dome is smoother.
10. The lowest point of the subperipheral portion of the outer apertural lip is closer to the umbilicus.

A comparison of this list with the tabulation of allometric trends in ontogeny (Chapter 4) demonstrates that, for eight of ten points, these samples possess at large sizes features which characterize earlier ontogenetic stages of *P. bermudensis zonatus.* The two exceptions are readily resolved into the general interpretation.

a) After reaching an early maximum, umbilical width remains constant during ontogeny. Umbilical width is a mechanical correlate of relative shell width at the point in growth at which umbilical width becomes maximal. The differential growth ratio, although lowered in these samples, is still considerably greater than 1, and relative height of the post-embryonic spire increases continually during growth. Since relative height at 30 mm is a good deal less in these samples than in *P. bermudensis zonatus,* relative width at the point of maximal umbilical width will likewise be greater than relative width at the corresponding point in *P. bermudensis zonatus.*

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[1] Although the justification for separate subspecific status will be presented in section C, the names are introduced here to facilitate referencing in discussion.

Hence, the umbilicus of these samples will be absolutely wider.

b) The differential growth ratio is constant during the growth of an individual. The power function applies from the termination of whorl 2 to the end of growth. From hatching to the end of whorl 2, growth in relative width is remarkably rapid, transforming the quadrate protoconch (Pl. 3, fig. 6) into a disk-like juvenile. The differential growth ratio is low at first, increasing gradually until its value becomes stabilized. Lowered differential growth ratio can be interpreted as a retention of juvenile growth rates.

The mere enumeration of a list of differences is worth little without an assessment of redundancy among its items, for all entries in an impressive tabulation may measure a single dimension of variation.

Not all the 10 components of the foregoing list are independent. The low spire is produced by a low differential growth ratio and implies, in turn, a relatively wide aperture. A shell with a low spire and relatively wide aperture will be relatively wide in general, from which the production of an absolutely wide umbilicus can be inferred. Items 4 through 8 measure only one aspect of variation. When the redundancies are eliminated, however, there remain at least four groups of variables which, in 8-axis oblique factor solutions (see Chapter 5), generally sort separately. These are:

a) measures of color (item 1)

b) the callus (item 3)

c) measures of form ratio (items 4–8)

d) conformation of the subperipheral portion of the outer apertural lip (item 10).

To say that there are at least four separate dimensions of variation in the list is not to assert that the four are unrelated. All are linked in ontogeny, since small shells of *P. b. zonatus* are weakly colored, lack a callus, are relatively wide, and have the lowest portion of the outer apertural lip at the umbilical border (Pl. 4, fig. 2). It is certainly a significant datum that a group of traits which normally occur together in juvenile shells of an ancestor maintain their association and reach the same values at maximal sizes in descendants. This can be interpreted in only one way—the subspecies are paedomorphic branches of the central stock, *P. bermudensis zonatus*. *Every* characteristic ontogenetic feature developed at or after the fifth whorl in these subspecies is attained by whorl 3–4 in *P. bermudensis zonatus*.

Two objections often raised to hypotheses of paedomorphosis are either invalid or inapplicable to this case:

a) Paedomorphosis has been proposed to explain the presence in adult descendants of one or a small group of features that typify earlier stages of ancestral ontogeny. That the hair distribution of human adults is similar to that of fetal chimpanzees need not imply that hair loss in human evolution occurred by embryonic retention, but rather that less hairy individuals were selected from the static spectrum of variation at adult sizes. This will not apply to the large specimens of these paedomorphic subspecies, which are scaled-up replicas of earlier stages in the ontogeny of *P. bermudensis zonatus* (Pl. 4, fig. 2 and figs. 3–6). Whereas the similarity in shape between a single trait of a young ancestor and adult descendant can easily be attributed to coincidence, the probability that such an explanation could apply to every measurable feature of ontogeny is effectively nil.

b) By a curious *non sequitur*, the citation of adaptive significance for an evolutionary change has been judged a denial of paedomorphosis as the mode of alteration. Paedomorphosis, is, in de Beer's phrase (1958: 36), a "morphological mode" by which selection can operate to produce adaptive adult configurations. If a thin shell, weak coloration, relatively wide shell, or any combination of these was favored by selection, paedomorphosis is one mode among many by which the change could have been effected.

C) Paedomorphosis Occurred at Least Four Times

The proposition that two taxa, one a paedomorphic derivative of the other, inhabited Bermuda during the Shore Hills-Southampton interval is the simplest phyletic interpretation that can be given to the distribution of paedomorphic samples; this interpretation is implicit in earlier work. Gulick (1904) and Verrill (1905) realized that fossil and modern *P. bermudensis* were distinguishable, and assumed a simple unilinear derivation, since they did not find paedomorphic fossils. Gulick even recognized, for the wrong reasons, that modern shells resembled earlier ontogenetic stages of fossil forms: "Thus in their smaller number of whorls [this is not true], their less rounded contour [by which he means less strongly domed, not rougher in cross-sectional outline], and their [relatively] larger umbilicus, the present snails seem like an undeveloped or degenerate race of the former species" (Gulick, 1904: 419). As paedomorphic fossils were discovered, the notion that two closely related species persisted throughout the preserved Pleistocene sequence gained favor: Peile (1926) listed *P. zonatus* and *P. bermudensis* in his synopsis of the subgenus.

I found a more complex story, involving an unusually literal interpretation of paleontological data. Each of the four discontinuous occurrences represents an independent episode of paedomorphosis. Evidence for separate origins will be presented with reference to Figures 17–19, Q-mode plots for all measured samples of *P. bermudensis.* Numbers on these plots correspond to the following samples:

a) Shore Hills non-paedomorphs: 01, 02, 02, 04

b) Shore Hills paedomorph (*P. b. fasolti*): 05

c) Harrington non-paedomorphs: 06, 07, 08, 09, 10

d) Harrington paedomorphs (*P. b. sieglindae, P. b. siegmundi*): 12, 13

e) Pembroke non-paedomorphs: 11, 14, 15, 16

f) Pembroke paedomorph (*P. b. sieglindae*): 17

g) St. George's non-paedomorphs: 18, 19, 20, 21, 22

h) St. George's paedomorph (*P. b. bermudensis*): 23

i) Southampton non-paedomorphs: 24, 25, 26, 27

j) Southampton paedomorphs (*P. b. bermudensis*): 28, 29, 30

k) Recent paedomorphs (*P. b. bermudensis*): 31, 32, 33, 34, 35, 36.

The Shore Hills paedomorph shares with other samples of its geologic formation those unique morphological features that separate these oldest *P. bermudensis* samples from all others. Shore Hills shells are distinguished by their small size at a whorl,[1] their remarkably flattened apex (measured by the initial form index), and low values of the lower eccentricity (Table 11 and Chapter 4 for definition of measures). Other morphological consequences ensue: the flat apex produces a low spire, a relatively wide shell, and a wide umbilicus. Shore Hills samples of *P. b. zonatus* are maximal among non-paedomorphs in umbilical widths; *P. b. fasolti* exceeds all other paedomorphs in this measure. Shore Hills *P. b. zonatus* are relatively widest among non-paedomorphs at the fifth whorl; *P. b. fasolti* surpasses all other paedomorphs in relative width. The lower eccentricity of Shore Hills *P. b. zonatus* is lower than that of all more recent non-paedomorphs; no post-Shore Hills paedo-

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[1] This serves to emphasize the fact that large whorl size does not imply large maximal size. Shore Hills shells grow to absolutely larger sizes than all more recent *P. bermudensis*, despite their smallest size at a whorl—i.e., they have more whorls at maximum sizes.

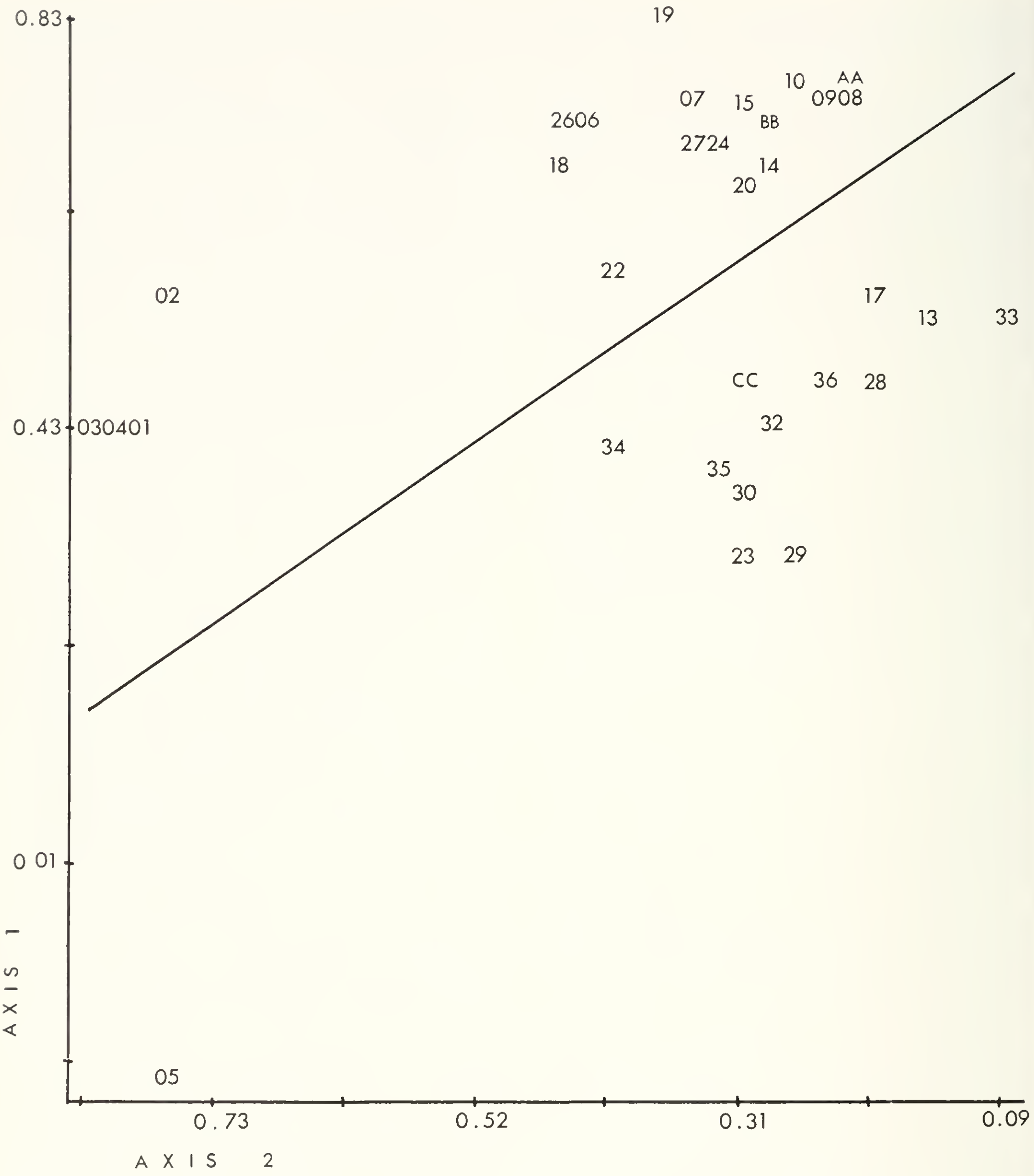

Figure 17. Plot on varimax axes of all *P. bermudensis* samples. AA stands for 11 and 21, BB for 16 and 25, CC for 12 and 31. Diagonal line separates all non-paedomorphs (above) from all paedomorphs (below).

morph attains a value of this variable as low as that of *P. b. fasolti* (etc. for the entire set of features distinguishing paedomorphs from non-paedomorphs). The extent of the morphological gap separating Shore Hills from later samples is evident in Figure 17. (The arbitrary oblique line of this figure divides paedomorphs from non-paedomorphs; note the distance between *P. b. fasolti* and the other three paedomorphic subspecies.)

The postulate that Harrington paedo-

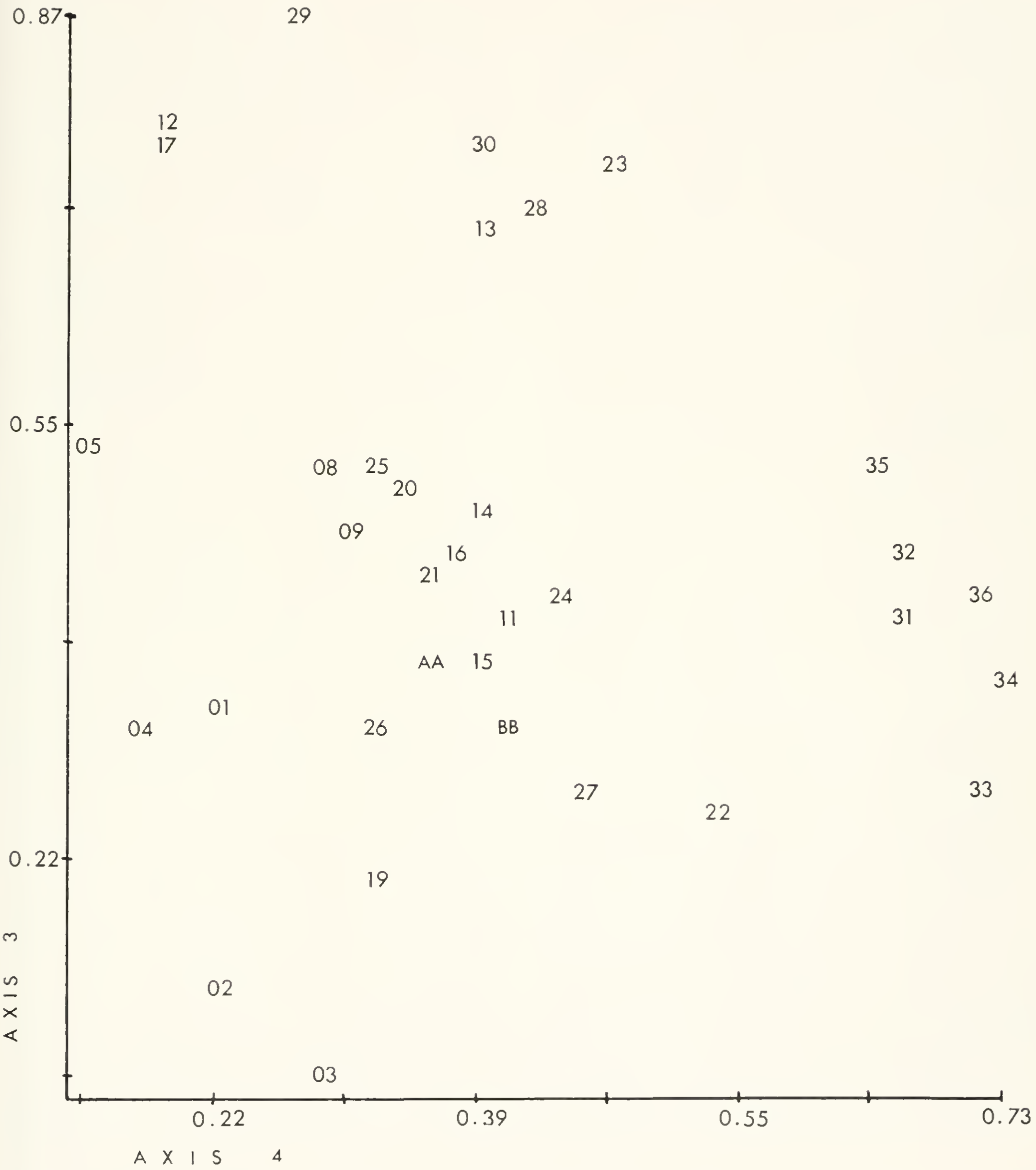

Figure 18. Plot on varimax axes of all *P. bermudensis* samples. Fourth axis separates modern *P.b. bermudensis* (31–36) from all other paedomorphs. AA stands for 07 and 10, BB for 16 and 18.

morphs evolved directly from *P. b. fasolti* involves the improbable hypothesis that the unique features of Shore Hills samples were modified twice in exactly the same manner. The parallel modification of large numbers of variables is not in itself improbable and must occur if paedomorphosis in *P. bermudensis* is recurrent, as proposed here. Frequent development of the many traits characterizing paedomorphic shells

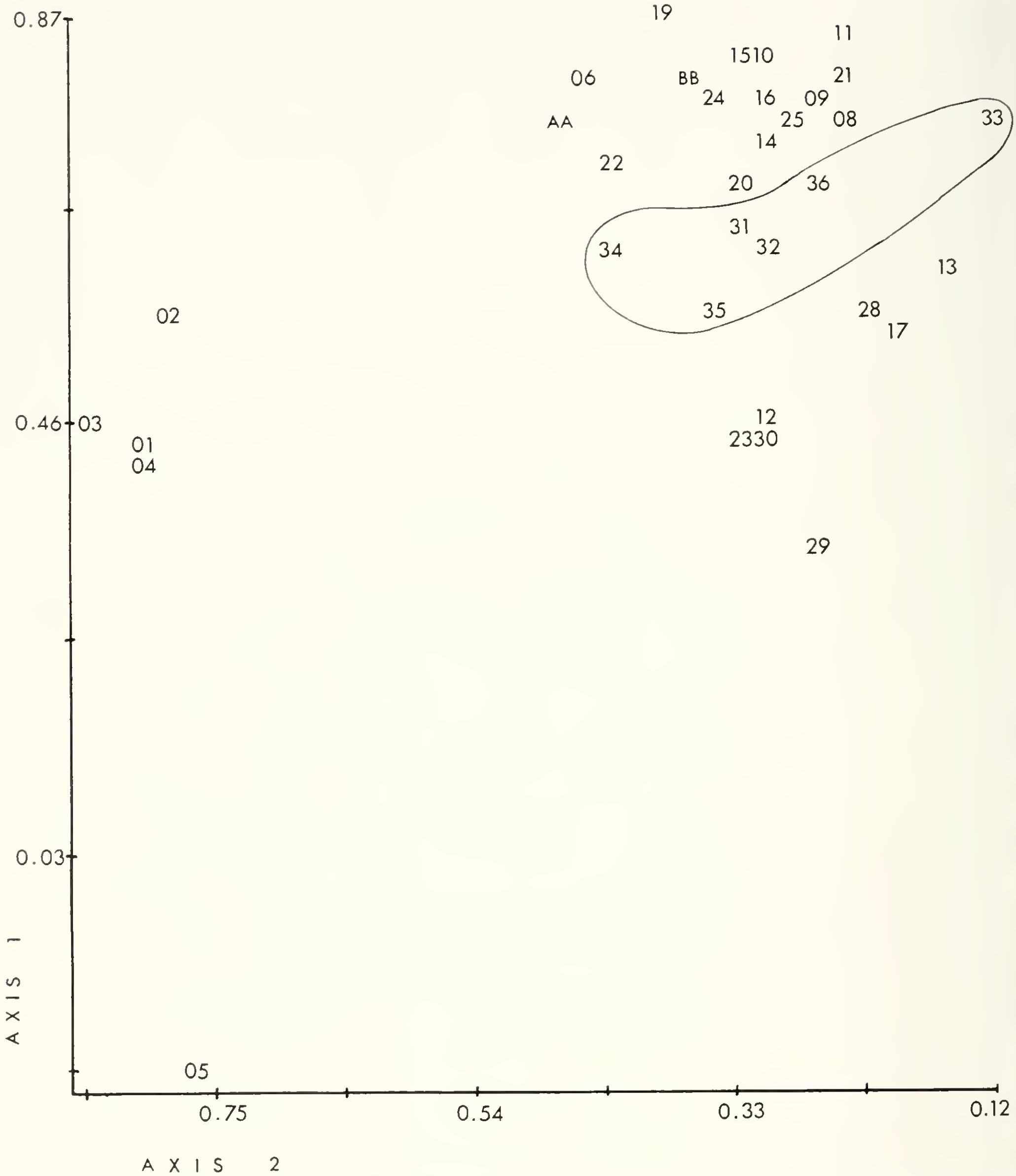

Figure 19. Plot of all *P. bermudensis* samples. Modern *P.b. bermudensis* circled; note intermediate position between post-Shore Hills paedomorphs and non-paedomorphs. AA stands for 18 and 26, BB for 07 and 27.

has a potentially simple genetic base, but a double origin of Harrington *P. bermudensis* would involve the similar independent development of many unrelated features. Increase in whorl size will not mechanically produce a more convex spire and, if anything, should bring about a *decrease* of the lower eccentricity, for large shells at a whorl have fewer whorls at the standard size, and the positive correlation

TABLE 11. *P. BERMUDENSIS*: COMPARISON OF SHORE HILLS SAMPLES WITH MORE RECENT SAMPLES. Figures cited are ranges of mean sample values in mm.

	Shore Hills	More Recent
Size at the fifth whorl	12.85–13.99	14.47–16.77
Initial form index	0.158–0.186	0.207–0.293
Umbilical width:		
paedomorphs	3.01	1.82–2.51
non-paedomorphs	2.22–2.40	1.69–2.22
Lower eccentricity:		
paedomorphs	0.182	0.256–0.446
non-paedomorphs	0.318–0.380	0.425–0.528

of lower eccentricity is stronger with whorl numbers than with size. When all measured features are considered, the Harrington paedomorphs are more similar to Harrington non-paedomorphs than to *P. b. fasolti*, which is best regarded as a short-lived branch derived from Shore Hills *P. bermudensis zonatus* (Fig. 20).

In Harrington times, paedomorphic populations evolved at the range peripheries of eastern and western *P. bermudensis zonatus*. *P. b. siegmundi*, found in two localities on Ireland Island, displays the typical western color pattern—023 with band formation delayed; *P. b. sieglindae*, bearing the 123 pattern, arose at Rocky Bay in the southwest corner of the range of eastern snails. Since eastern and western stocks were evolving separately during the Shore Hills-Southampton interval, the two paedomorphs are independent developments.

Another eastern paedomorph, *P. b. bermudensis*, evolved in St. George's time on what is now St. George's Island in northeast Bermuda. The proposal for an origin of this form separate from that of *P. b. sieglindae* is weaker than previous cases of distinct derivation. Yet I maintain this view for the following reasons:

a) *P. b. bermudensis* evolved at a range periphery of *P. b. zonatus* opposite from the point of origin of *P. b. sieglindae*.

b) *P. b. sieglindae* seems to have been a small, isolated, and short-lived population. It extends only from the uppermost Harrington to the lowest Pembroke and was probably annihilated by the strong growth of Pembroke dunes. In lower Pembroke times, its range is narrowly limited to the east and west by populations of *P. b. zonatus* at localities 2 and 47; the entire east-west extent of its Pembroke range could not have exceeded 200 meters.

I conclude that the *P. bermudensis zonatus* stock branched at least four times during the Shore Hills-St. George's interval, that each branch is a paedomorphic derivative of the central stock, and that an extensive set of similar and non-redundant morphological features therefore evolved many times and independently. This heterochronous parallelism or "iterative evolution"[1] has been documented in other fossil groups. It is best known among Mesozoic ammonoids and in the repetitive development of the ostreid form genus *Gryphaea*. Iterative trends in the evolution of brachiopod lophophores have been documented by Elliott (1948), who cites further cases among echinoids and foraminifera. Standard objections to such hypotheses involve the "complexity" of morphological alteration (usually defined in terms of the number of differences that can be cited) and the improbability of its repetitive occurrence. But complexity is not a matter of simple enumeration; in this case many characters are involved, but the change has a simple genetic and ontogenetic basis —the very prerequisites listed by Simpson (1953: 251) for the occurrence of iterative trends.

Rensch (1937) has provided an interesting analogy that should dispel qualms as to the improbability of independent origin for markedly similar shapes. In western

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[1] Simpson's definition (1953: 248) of iterative evolution fits this example particularly well: "The repeated occurrence of similar trends in successive offshoots of a group, often form a continuing 'conservative stem.' "

Sicily are found flattened, carinate, umbilicate subspecies of six genera that are normally smooth, rounded, and non-umbilicate in the manner of such typical helicids as *Otala*. Moreover, "similarity among the carinate races, which have arisen independently in parallel fashion, is so great that, on the basis of the shell alone, *Murella muralis scabriuscula*, *Tyrrheniberus villica sardonia*, and *Rossmaessleria subsc. subscabriuscula* could be considered as races of a single species. Such cases are of great significance for paleontology" (translated from Rensch, 1937: 587). Here similarity among derived subspecies of three genera is stronger than that among the four paedomorphic subspecies of *P. bermudensis*, for only between an uncallused *P. b. sieglindae* and *P. b. bermudensis* could any difficulty of identification arise in well-preserved specimens. The uncanny aspect of Rensch's example is that the passage from rounded, non-carinate forms to sharply keeled derivatives is reminiscent of the transition from *P. b. zonatus* to its paedomorphic branches. Yet it is analogy only, for Rensch's carinate forms are not derived by paedomorphosis and seem for the most part to have thicker shells than typically-shaped subspecies.

The emphasis on simplicity of genetic and ontogenetic production of paedomorphic forms raises another important issue: Granted that the four branches are distinct and paedomorphic, does the change have any genetic basis? Is this case merely another *Ambystoma*-axolotl, a phenotypic response to a given set of environmental conditions? If this were true, its recurrence would be a matter of no great interest. It seems not to be true for the following reasons:

a) Geographic and temporal distribution of paedomorphic forms is consistent with their constitution as taxonomically-significant biological populations.

i) As would be expected under current notions of geographic speciation, the origin of a paedomorphic offshoot invariably occurs at the periphery of the known range of its parental form (Mayr, 1963; Chapter 16). This is least well documented for *P. b. fasolti*, since the geographic range of Shore Hills populations is so small. Still, this paedomorph is found at the northern extent of the known species range and is more widely separated from its nearest conspecific neighbor than are any other two collections of this age. *P. b. siegmundi* arose at the extreme northwest extent of western *P. b. zonatus; P. b. sieglindae* at the southwest corner of the range of eastern non-paedomorphs. *P. b. bermudensis* had its origin at the northeast periphery of the known range of eastern *P. b. zonatus.*

ii) During the entire St. George's-Southampton interval, *P. b. bermudensis* evolved in isolation on what is now St. George's Island. For a period of up to 120,000 years, paedomorphs and non-paedomorphs occupied non-overlapping geographic ranges in which environmental conditions could not have differed widely.

b) Many living populations of *P. b. bermudensis* have re-acquired features characteristic of ancestral *P. b. zonatus.* In particular, the shell has become thicker and relatively higher (through an increase of the initial form index with no significant modification of the differential growth ratio), and color is intensified so that all three bands have usually formed by the fifth whorl.[1] However, some of the morphological consequences that invariably follow such trends in *P. b. zonatus* do not ensue. A thickened shell invariably produces a stronger callus in *P. b. zonatus;* no callus forms in *P. b. bermudensis.* More important, a recognizable percentage of shells in *all* post-Shore Hills samples of eastern *P. b. zonatus* display the color variation "faded."

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[1] Figure 17 does not distinguish modern *P. b. bermudensis* from other post-Shore Hills paedomorphs, but high projections on the fourth axis differentiate the modern samples from all older forms (Fig. 18). In a plot of axis 1 vs. axis 2 of a 4-axis solution, modern *P. b. bermudensis* samples lie midway between the clusters of all post-Shore Hills paedomorphs and *P. b. zonatus* (Fig. 19).

(Pl. 5, fig. 5). This variation, which appears *after* the flame-band transition (usually during development of the fifth whorl), is necessarily absent from paedomorphs that are still in the flame stage at maximal sizes. *P. b. bermudensis* exhibited this weakened coloration during the entire St. George's-Southampton interval; modern *P. b. bermudensis,* which have re-acquired coloration equal in strength to typical *P. b. zonatus*, never display the "faded" variation. I assume that genetic determinants of the callus and "faded" variation were lost from the *P. b. bermudensis* gene pool during the lengthy period in which shells never reached a developmental stage sufficiently advanced for their phenotypic manifestation. In addition to the implication that there exist genetic differences between paedomorphs and non-paedomorphs, this example helps to answer another question: If non-paedomorphs gave rise to paedomorphs four times, why is the reverse transition unknown? Paedomorphosis is a one-way street. Non-paedomorphs must, by definition, possess the capacity for production of the paedomorphic phenotype, for it already exists as an early ontogenetic stage. Paedomorphic populations, on the other hand, will tend to lose genes for features of late ontogeny which can never be brought to phenotypic expression.

Since the four paedomorphic offshoots occupy geographic subdivisions of the species range and differ genetically from the parental stock, separate taxonomic status is warranted. Although defensible on purely morphological grounds, the erection of a single subspecies for the paedomorphs is inadmissible. A form genus is pardonable (since that category is not "real"), but a form subspecies violates population concepts. Therefore, each paedomorphic offshoot has been given separate subspecific status. A visual reconstruction of the evolutionary history of *P. bermudensis* is presented in Figure 20; two of a set of data portrayals according to this scheme constitute Figures 21–22.

D) Cause of Paedomorphosis

1. *Efficient cause.* Rothschild and Rothschild (1939) showed that pulmonates whose gonads had been partly or completely destroyed by parasitic trematodes tended to grow faster and attain larger maximal sizes. Growth curves of many pulmonates display a sharp nick at the point of gonad maturation, indicating a rapid decrease in the growth rate (Boettger, 1952: 469). This rapid slowing of the juvenile growth rate is often accompanied by the development of morphological features that characterize adult forms. Parasitically castrated individuals of *Helix pomatia*, *Arianta arbustorum*, and *Bradybaena fruticum* do not develop typical features of the adult aperture—thickening, coloration, and change in direction of growth (Boettger, 1952). The prolongation of rapid juvenile growth rates may therefore delay the formation of adult characters and produce paedomorphic effects.

If maturation in paedomorphic *P. bermudensis* subspecies occurred at the same number of days after hatching as in non-paedomorphs but at a larger size (due to slower pre-maturational diminution of initially rapid growth rates), then the intensity of gradual allometric alterations that produce typical form differences between juveniles and adults might be correspondingly diminished. Juvenile rates of development would persist longer (in terms of size, though not of time), and such a form, when compared with a typical specimen at a corresponding size near maximum size, would be paedomorphic. The same morphological effect would arise from an absolute delay of maturation in paedomorphs (in time after hatching relative to non-paedomorphs). Thus, paedomorphs either grow faster and mature at the same time as non-paedomorphs, or mature later and thereby prolong the same juvenile growth rate to larger sizes.

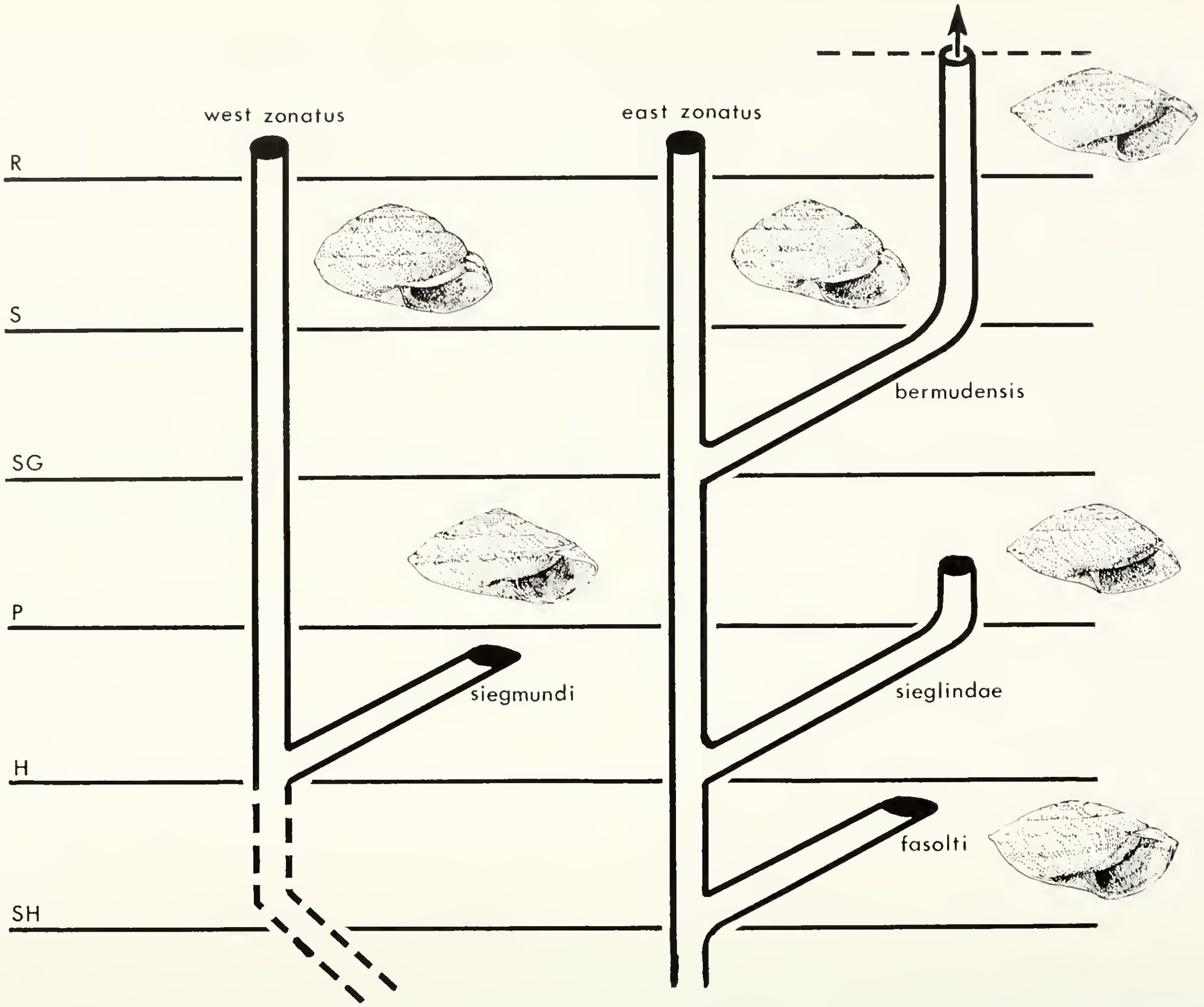

Figure 20. Reconstruction of the phyletic history of *P. bermudensis* showing iterative development of paedomorphic subspecies. SH = Shore Hills; H = Harrington; P = Pembroke; SG = St. George's; S = Southampton; R = Recent.

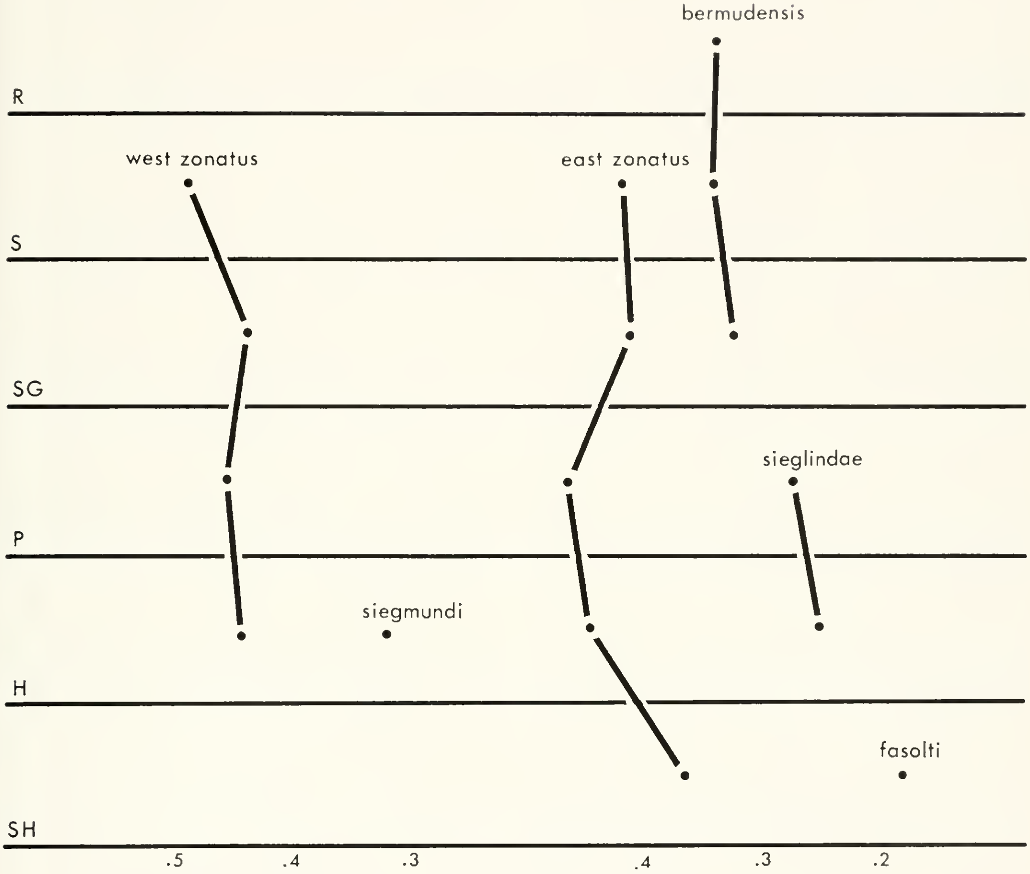

Figure 21. Values for lower eccentricity in *P. bermudensis* displayed in phylogenetic framework. Cited figures are means of mean sample values. SH = Shore Hills; H = Harrington; P = Pembroke; SG = St. George's; S = Southampton; R = Recent.

The weakness of coloration in large paedomorphic shells of *P. bermudensis* can be interpreted in two ways: flames (rather than a band) are produced either because pigmentation is more limited or because a rapid growth rate "spreads thinner" a quantity of pigmentation whose deposition rate is constant per unit of time. Comfort (1951) indicates that this second explanation often applies to pulmonates: "The intensity of pigmentation varies with the growth rate, periods of diapause giving rise very often to darker varices, and periods of rapid growth to paler zones." Likewise, thickness of the callus seems to increase during growth pauses; a sufficiently rapid general growth rate might prevent its formation altogether and, as a further consequence, produce the relatively thin shell characteristic of paedomorphs. I suggest, therefore, that a prolongation of rapid juvenile growth rate (and, by implication, juvenile patterns of ontogenetic allometry) to later sizes is responsible for paedomorphosis in *P. bermudensis*. Since the paedomorphic subspecies reach the same maximal size and whorl number as non-paedomorphs, features which form

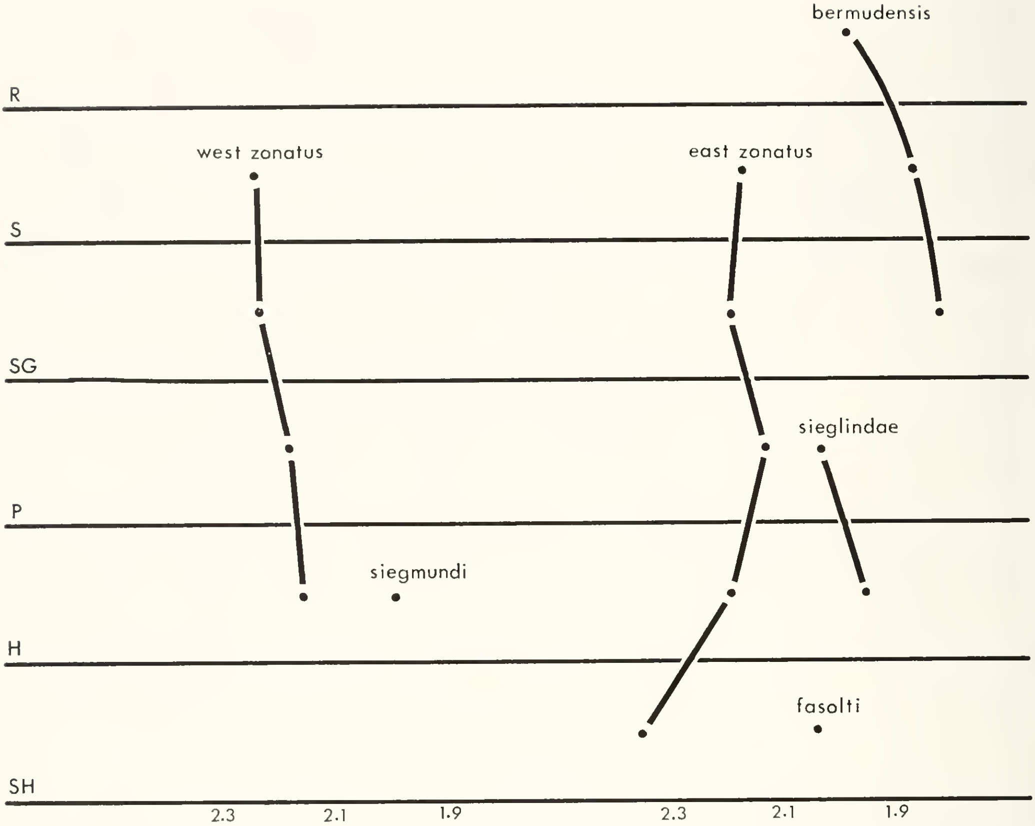

Figure 22. Values for differential growth ratio in *P. bermudensis* displayed in phylogenetic framework. Cited figures are means of mean sample values. Formational symbols as in Figure 21.

during the fourth and fifth whorl of non-paedomorphs are so delayed in appearance that they never form in paedomorphs.

2. *Adaptive significance.* There is an interesting correlation between the incidence of paedomorphosis and depositional environment:

a) Paedomorphosis is most advanced in subspecies originating in red soils. *P. b. fasolti* and *P. b. bermudensis* never possess a callus and rarely (with the exception of some living *P. b. bermudensis*) develop band 1 or 2.

b) Paedomorphosis is less pronounced in subspecies originating in unindurated zones. Bands 1 and 2 are slightly delayed but usually form in *P. b. siegmundi* and *P. b. sieglindae;* a callus is weakly developed in both subspecies.

c) Paedomorphs never originate in eolianites. (*P. b. bermudensis*, living in isolation, survived the period of Southampton dune building, but its geographic separation from competition renders an assessment of its relative adaptability to such an environment impossible).

Red soil conditions seem to favor paedomorphosis; moreover, as will be discussed in the next chapter, both *P. bermudensis zonatus* and *P. nelsoni* tend to have thinner shells in Shore Hills and St. George's times. This may suggest that paedomorphosis served as one pathway to the attainment of a thinner shell, which would have been adaptive in the limited calcium environment of red soils (Oldham, 1934; Lozek, 1962). That paedomorphosis is not an unreasonably indirect or difficult pathway to such an adaptation is indicated by an R-mode factor analysis of the matrix of means for all *P. bermudensis zonatus* samples. Since non-standardized variables are considered at a uniform size (height + width = 30 mm), the matrix to be factored is analagous to a partial correlation matrix of inter-sample variability with the effect of size removed. The axis 2 grouping of a 7-axis solution includes: aperture width/aperture height and width at fifth whorl/height at fifth whorl projecting positively, and callus thickness, aperture height, and lower eccentricity projecting negatively. Even among non-paedomorphs, a relatively wide shell is associated with a weak callus and a low value of the lower eccentricity. General developmental accelerations and retardations seem to occur within the *P. bermudensis zonatus* stock, whose pattern of intersample variation therefore suggests the latent potential for paedomorphosis— a more pronounced developmental retardation.

IX. PHYLETIC EVOLUTION OF *P. BERMUDENSIS ZONATUS*

A) Climate and Evolution in Land Snails

Glacially-controlled oscillation of climate and sea level is the independent variable of Bermuda's Pleistocene history. Neither stratigraphy nor paleontology can proceed much beyond the descriptive without reference to its effects. The cyclothem of Bermudian geology—glacial red soil (solutional unconformity) → interglacial carbonate (eolianite and marine limestone)—is an expression of this oscillation. The temporal recurrence of similar environments leads us to ask whether the morphology of fossils also records the alternating selective pressures of a fluctuating climate. Parallel oscillation of climate and morphology has been recorded in several studies of Pleistocene evolution (in Kurtén's work on fluctuating size trends in fossil bears and, in particular, the changes in coiling-direction frequencies in planktonic Foraminifera—see e.g. Jenkins, 1967).

The relationship of morphology and environment, central to any evolutionary theory, was a subject of intense debate during the late 19th century—a discussion in which land snails figured prominently. J. T. Gulick (1873, 1905) disputed the Darwinian view that geographic variation in the morphology of a species should be referable to selective pressures exerted by environmental differences. From studies on the distribution of *Achatinella* in Hawaii, he concluded that morphological differences arise in identical environments and that geographic separation is a sufficient cause and not merely a precondition of speciation. "The evolution of many different species may take place without any difference in the food, climate, or enemies that surround them . . . Separation without a difference of external circumstances is a condition sufficient to ensure variation" (Gulick, 1873: 504–505).

In defense of the selectionist thesis that he had co-authored, Wallace (1899: 148) replied:

> It is an error to assume that what seem to us identical conditions are really identical to such small and delicate organisms as these land molluses, of whose needs and difficulties at each successive stage of their existence, from the freshly-laid egg up to the adult animal, we are so profoundly ignorant. The exact proportions of the various species of plants, the numbers of each kind of insect or of bird, the peculiarities of more or less exposure to sunshine or to wind at certain critical epochs, and other slight differences which to us are absolutely immaterial and unrecognizable, may be of the highest significance to these humble creatures, and be quite sufficient to require some slight adjustments of size, form, or colour, which natural selection will bring about.

This debate extended beyond snails and beyond the role of selection in evolution, for basic intellectual attitudes were involved. As originally formulated, the

Darwinian approach was highly deterministic in accord with prevailing notions of the nature of natural science. To invoke the term "science" was to imply a deterministic model—witness the "scientific socialism" of Marx and its theory of ineluctable historical progression. This attitude is quite explicit in Wallace's rebuttal of Gulick:

> If the average characters of the species are the expression of its *exact adaptation* to its whole environment, then, given a precisely similar environment, and the isolated portion will *inevitably* be brought back to the same average of characters (Wallace, 1889: 149; my emphases).

Rev. Gulick was a participant in the late 19th century antimechanist reaction which, in another guise, culminated in vitalism and the "creative evolution" of Henri Bergson:

> If my contention [that different species of a genus can arise in identical environments] is in accord with the facts, the assumption which we often meet that change in the organism is controlled in all its details by change in the environment, and that, therefore, human progress is ruled by an external fate, is certainly contrary to fact (Gulick, 1905: iv).

Our contemporary reconciliation, which has affirmed and extended the role of selection within the non-mechanist framework of modern evolutionary theory, has incorporated much of Gulick's attitude and some of his empirical conclusions (e.g., the emphasis on geographic isolation in speciation).

Amidst the excitement provoked by rediscovery of Mendel's work, Crampton (1916) again focused on the relationship of environment and morphology in his study of *Partula*. The "causal value of the 'environment' in producing varietal modifications" was, to Crampton (1916: 48), the "major problem." He concluded:

a) "The originative influence of the environment seems to be little or nothing" (1916: 12).

b) "The morphological differences observed are due to spontaneous congenital causes that remain unknown in themselves, but whose effects are produced quite independently of the external conditions" (1916: 48).

Darwin had answered only one of the two great questions; he had explained the production of new forms by natural selection of variants but had not discovered the source of variation—and this "Origin of the Fittest" (as Cope entitled his book) was to many evolutionists the more important issue. The early mutationists thought they had found the key to this origin in Mendel's laws (second quote above) and relegated natural selection to the non-creative function of headsman:

> The role of the environment is to set the limits to the habitable areas or to bring about the elimination of individuals whose qualities are otherwise determined—that is, by congenital factors (Crampton, 1916: 311).

Both neo-Lamarckians and early mutationists denied selection a creative role, the former because variation was inherently directed towards adaptation, the latter because adaptations arose in a single step. The truly creative function of selection, continual and successive preservation of the adaptive component from a random spectrum of variation, was perceived by neither. Crampton remarked: "Some among the neo-Darwinians endeavored to make natural selection originative as well as discriminatory, but their views have not gained wide acceptance" (1932: 187).

It is ironic that Crampton, in his efforts to discredit neo-Larmarckism by denying to the environment an "originative influence," joined Cope and Osborn in failing to grasp the importance of selection. To deny direct environmental induction is not, of course, to eliminate the possibility that morphology and environment are related, for the role of environment is to determine the direction of selection.

In the initial stages of its development, a new theory is often taken by its proponents as all-encompassing; only later are syntheses effected with the cogent aspects of earlier views. In assigning to mutation

TABLE 12. CORRELATION OF MORPHOLOGY AND CLIMATE IN *P. BERMUDENSIS ZONATUS*: FLUCTUATING TRENDS IN WHORL SIZE AND SHELL THICKNESS. Total number of specimens and number of samples shown under column headed N; the means and ranges cited in the table are compiled from mean sample values. In the tabulation of ranges, the value of the anomalous Spittal Pond St. George's sample is recorded separately, but included in the calculation of the mean. For this sample, size at the fifth whorl is 16.35 mm; callus thickness is 0.177 mm. All measures in mm.

	N	Size at Fifth Whorl	Callus Thickness
Southampton	62 (4)	16.28 (15.74–16.77)	0.383 (0.236–0.551)
St. George's	65 (5)	14.93 (14.47–14.67)	0.138 (0.010–0.229)
Pembroke	68 (4)	16.00 (15.71–16.41)	0.233 (0.193–0.295)
Harrington	95 (5)	15.45 (15.30–15.82)	0.279 (0.259–0.341)
Shore Hills	76 (4)	13.42 (12.85–13.99)	0.180 (0.141–0.223)

("spontaneous congenital factors") the role of both material *and* efficient cause of evolutionary change (instead of just the former as agreed today), Crampton failed to appreciate the indirect influence of environment in producing evolutionary change.

With the infusion of population concepts into evolutionary thought, the adaptive nature of geographic variation in land snails has become accepted. Welch (1938, 1942, 1958) studied the Hawaiian *Achatinella* anew and in far greater detail than Gulick had done. He found definite correlations of form and size with altitude, moisture, and temperature among subspecies of *Achatinella mustelina* (Welch, 1938). Bailey (1956) attributed some of Crampton's "non-adaptive" variation to the results of selection. Studies were made of the phenotypic effects of different environments upon land snail shells (Oldham, 1934; Rensch, 1932) and results were used to interpret genetically determined variation in adaptive terms (Rensch, 1937). Work on *Cepaea* demonstrated that the distribution of color variation corresponds well with inferred environmental selective pressures (review in Harvey, 1964; Ford, 1964).

While so much excellent work on the adaptive nature of infraspecific geographic variation has been produced, virtually nothing is known of the nature of temporal variation within pulmonate species. Pulmonate paleontologists have confined their climatic concerns to species distribution patterns and have not studied morphological variation within a species living through a temporal succession of environments (reviews in Lozek, 1965; Taylor, 1965; and la Rocque, 1966). Temporal variation in *P. bermudensis zonatus* will be considered in this chapter.

B) Correlation of Environment and Morphology

Unlike that of *P. nelsoni*, the morphology of *P. bermudensis zonatus* exhibits no immediately recognizable correlation with lithology and, by implication, climate. However, a highly significant pattern can be inferred from the measurements. This pattern parallels noted trends of the *P. nelsoni* stock and proves that glacial and interglacial climates are associated with characteristic morphologies in four lines (*P. nelsoni*, *P. superior*, eastern and western *P. bermudensis zonatus*).

a) shell thickness: Strength of the parietal callus is a good measure of relative shell weight. In Shore Hills (glacial) times, the callus of *P. bermudensis zonatus* was weakly developed at the standard size. Shell thickness increased during the succeeding interglacial (Harrington-Pembroke) only to fall again to Shore Hills levels with the return of glacial climates during the St. George's. The double oscillation was completed when Southampton (interglacial) snails reacquired strong calluses (Table 12, Fig. 23).

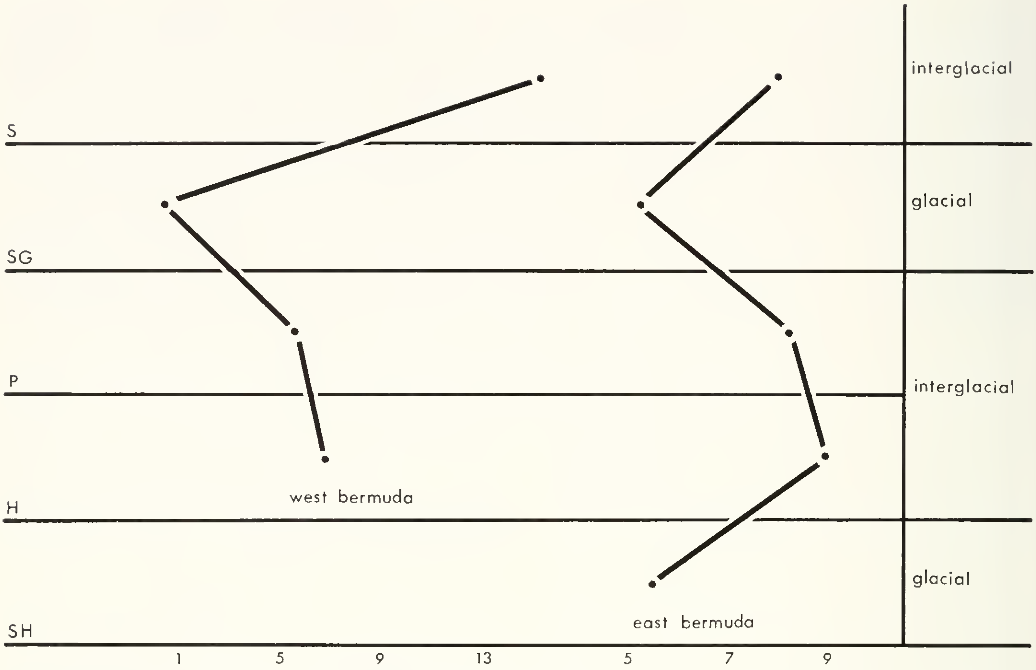

Figure 23. Correlation of shell thickness (callus) and climate in western (left) and eastern stocks of *P. bermudensis zonatus*. SH = Shore Hills; H = Harrington; P = Pembroke; SG = St. George's; S = Southampton.

b) shell size:

i) maximum size: With a range of maximal shell size far smaller than that of *P. nelsoni* or *P. cupula*, little can be done with this variable in *P. bermudensis* due to great differences in sample size. I can state with fair certainty only that the largest Shore Hills snails surpass those of all more recent populations in maximal size. For more recent forms, I compiled means for the five largest specimens in each sample. The only consistent result of this procedure is the artifact that larger samples tend to have larger mean values. Grand means for each post-Shore Hills formation are: Harrington, 34.3 mm; Pembroke, 34.4; St. George's, 34.2; Southampton, 33.5. The largest St. George's sample (Spittal Pond, locality 32) has fewer specimens than *any* of the measured interglacial samples. If the sample-size artifact controls values of the grand means, then an unbiased sampling procedure might predict that St. George's specimens tend to be somewhat larger in maximal size.

ii) standardized size-at-fifth-whorl: Parallel oscillation of size-at-fifth-whorl and lithology is pronounced and consistent (Table 12, Fig. 24). Values of this measure are low in red soils, intermediate in unindurated zones (Harrington) and high in eolianites (Pembroke, Southampton). In three localities, Harrington and Pembroke snails were found in continuous sequence, inches apart in direct superposition—a strong indication that genetic continuity was maintained during the lithologic transition. In all cases (*P. b. zonatus* from Whalebone Bay, locality 1, and Town Cut, locality 87, and *P. b. sieglindae* from Rocky Bay, locality 44), Pembroke samples exhibit larger mean sample values of size at fifth whorl (significant at 5 per cent level in all

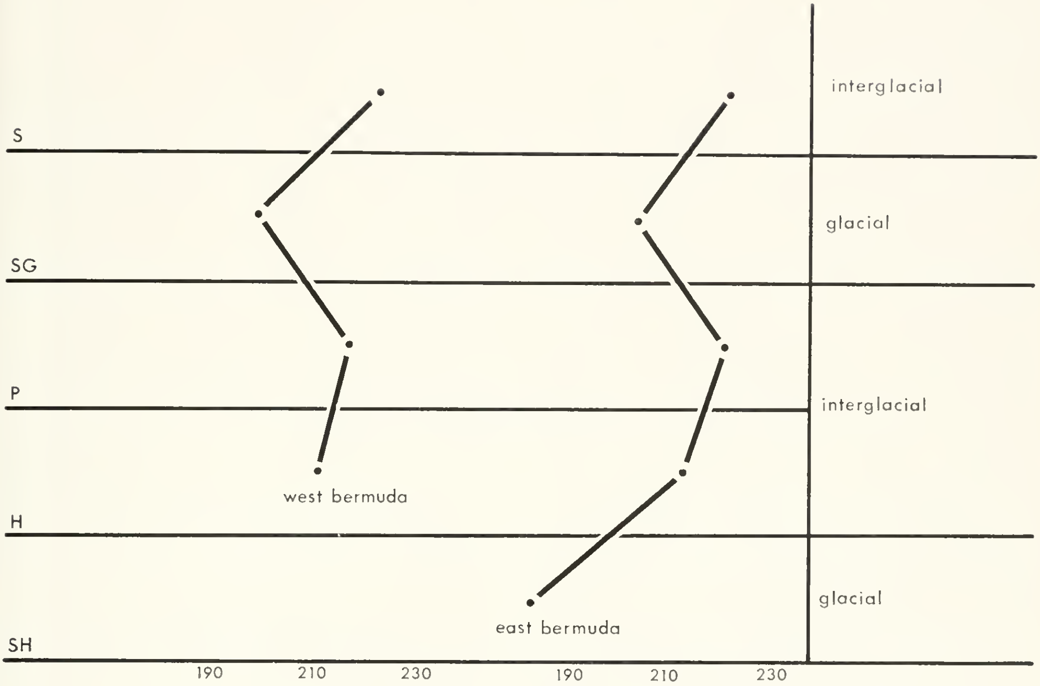

Figure 24. Correlation of size at fifth whorl and climate in western (left) and eastern stocks of *P. bermudensis zonatus*. Formational names as in Figure 23.

eases). The consistency of this correlation is even stronger than that for callus thickness. Leaving aside the St. George's Spittal Pond sample which is anomalous in all respects, the largest mean size-at-fifth-whorl for a red soil sample (14.67 mm, St. George's at Saucos Hill, locality 41) is a good deal less than the smallest eolianite value (15.30 mm, Harrington at Whalebone Bay, locality 1).

In conclusion, snails from red soils (glacial periods) tend to reach larger maximal sizes, have thinner shells and be smaller at a whorl than samples from eolianites.[1]

In *P. nelsoni*, apparent temporal fluctuations in morphology were interpreted as artifacts of an imperfect record. Two subspecies lived side by side from Shore Hills to St. George's and their alternating superposition in a single section reflects the migration of their preferred environments. I favor the literal interpretation of zig-zag evolution (Henningsmoen, 1964) for fluctuating trends in *P. b. zonatus* for the following reasons: The differences between red soil and eolianite *P. nelsoni* and *P. superior* are large and numerous (involving color—usually considered a better indicator of taxonomic distinction than form—as well as shape). The correspond-

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[1] As in *P. nelsoni*, small size at a whorl can be an artifact of small protoconch size, but this is not true here. Average protoconch widths for *P. b. zonatus* samples of all formations are remarkably similar. In another case, the decrease in whorl size of modern *P. b. bermudensis* compared with St. George's and Southampton forms, the artifact may be involved since living populations tend to have small protoconchs. Phyletic size decrease in *P. b. bermudensis* may be related to increased competition and decreased food resources caused by the recently introduced fauna (both human and pulmonate).

ing differences in *P. b. zonatus* are few and small, involving only those features which adapt the snail to its new environment (see next section) and only those magnitudes small enough to be encompassed by the phenotypic plasticity of a subspecies. I prefer the zig-zag hypothesis not because it is "simpler" *per se*[1] but because I would be surprised if the genetic determination of shell form is so precise that a local population cannot decrease the shell thickness of its members, but must give way to another already possessing the requisite thickness whenever such a modification is required by the conditions of life.

These single variable results are individual cases of a more general coherence. I had thought that quantitative appraisal of samples of this relatively conservative stock in a short time sequence might produce a haphazard clustering of samples, but Q-mode plots demonstrate that the samples of each temporal unit tend to associate. This may be due to the uniqueness of complex selective pressures in any given environment[2] or to genetic interchange among contemporaneous samples. The coherence, in any event, is an encouraging datum for the use of multivariate biometry in evolutionary studies.

The uniqueness of Shore Hills samples was demonstrated in Figure 17. To gain a better idea of subgrouping within the post Shore-Hills samples, I eliminated the Shore Hills data and ran another analysis. The numbers of Figures 25 correspond to the following samples: Harrington, 01–05; Pembroke, 06–09; St. George's, 10–13; Southampton, 14–17. As in *P. cupula* plots of Chapter 6, relative width of band 3 is the only color variable included; hence, distinction between eastern and western snails is not effected.

The St. George's red soil snails sort separately from eolianite samples. Within the eolianite cluster, Harrington samples (from an unindurated zone) are associated at the periphery of the cluster, closest to St. George's specimens. Samples from Pembroke and Southampton dunes are furthest removed from the St. George's snails. Only the anomalous Spittal Pond St. George's collection (number 13 — unintentionally) disrupts the general trend by grouping with the Pembroke snails.

C) Adaptive Significance of Oscillating Trends in Morphology

To learn the significance of this correspondence between morphology and lithology, we must discover what environments these lithologies imply and see how modern pulmonates vary in such habitats. Red soils were deposited on Bermuda during periods of continental glaciation; dune building occurred in interglacial environments (Bretz, 1960; Land, Mackenzie, and Gould, 1967). At a minimum, the environment of pulmonates living in red soils was, in comparison with that of eolianites,

a) colder

b) wetter (Bryan and Cady, 1934; J. Chase and A. MacIntyre, personal communication)

c) poorer in available calcium for shell building. Bermudian dunes are composed of calcareous organic fragments. The

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[1] Ockham formulated his razor to wield against the Platonic notion that universals existed in the real world. These universals were the entities that had been multiplied beyond necessity, and they were unnecessary precisely because they were inventions of the intellect. Thus, the razor, as used by Ockham and the early nominalists, was not a device to distinguish the better of two empirical postulates, but a method to simplify logic by the elimination of unnecessary non-empirical attributes. It is a shame that the razor is so often invoked improperly by modern scientists. We can all think of cases in which the more complex of two consistent empirical hypotheses provided a more satisfactory interpretation of a phenomenon. I do not deny that simpler explanations usually turn out to be more acceptable, but merely point out that the razor should not be cited as a *deus ex machina* to prove the case.

[2] Many simple selective pressures recur with similar basic environments, but the entire complex of pressures will not be exactly duplicated, if only because no two environments can ever be precisely alike.

Figure 25. Plot on varimax axes for all post-Shore Hills *P. bermudensis zonatus* (minus Ireland Island St. George's, for which only 5 specimens were available). Upper circle includes all Pembroke samples and the anomalous Spittal Pond St. George's. Lower circle includes all Harrington samples. 'Normal' St. George's at bottom.

$CaCO_3$ content of eolianites and unindurated zones ranges from 92.6 to 99.3 per cent (Ruhe *et al.*, 1961). Sayles (1931) determined the CaO content of a deep red phase and "pink variant" of the St. George's soil as 3.13 and 50.31 per cent, respectively. Ruhe *et al.* (1961) obtained values as low as 1.9 per cent for the $CaCO_3$ content of red soils.

The effect of these factors on pulmonate shells has provoked some interest and a widely scattered literature:

a) effect of temperature:

i) on maximal size: Likhachev and Rammel'meier (1952: 27) note that northern land molluscs of the USSR tend to be small. McGuire (1966), on the other hand, has stressed the adaptive advantages of large size at low temperatures. Most pulmonate workers are agreed that each form tends to have a temperature optimum above or below which maximum size decreases. Rensch (1932) found that several European species were characteristically smaller in regions of higher annual temperature. Since we cannot know the optima of extinct taxa, the effects of temperature cannot be inferred.[1]

ii) on shell thickness: J. W. Taylor (1900) and Likhachev and Rammel'meier (1952) noted a relationship between colder temperatures and thin shells, but Rensch (1932) could find no correlation between relative shell weight and temperature in his study of several European genera.

b) effect of precipitation:

i) on maximal size: Rensch (1932: 758) cites a large number of studies which indicate that local populations living in drier climates tend to reach smaller adult sizes than those of the same species in wetter regions. Geyer (1927, quoted in Rensch, 1932: 778) proposed that longer feeding periods between diapauses in areas of high rainfall tended to produce larger and thinner shells.

ii) on shell thickness: Geyer's conclusion has already been cited. Of all correlations between morphology and environment, Rensch (1932) found the strongest to be that of increased shell thickness with augmented solar illumination of dry climates.

c) effect of calcium availability:

Many authors have stressed the correlation of pulmonate distribution patterns with the presence of limestone outcrops. In calcium-poor areas of Czechoslovakia, Lozek (1962) has found snails crowded on the ruins of medieval castles and churches where disintegrating mortar furnishes a source of lime. Talmadge (1967) correlated the abundance of coastal land snails with the distribution of lime in drift shells, guano, subfossil marine shells, and Indian middens. On acidic islands off Nova Scotia, *Cepaea hortensis* obtains its lime from shells dropped by gulls (Bleakney, 1966). Many pulmonates are dependent upon direct ingestion of limestone for the construction of their shells. *Murella murella sicana* bores holes in limestone and incorporates the ingested material (which may comprise more than 90 per cent of the gut contents) into its shell (Rensch, 1932: 791–793). Rensch (1932) grew *Murella murella globularis* in a calcium-free environment; the shells produced were paper thin and the animals died before they were half grown. Snails so deprived of calcium will often eat empty shells (Rensch, 1932: 790; Smith, 1966: 248).

Oldham investigated the relationship between calcium availability and shell thickness for several genera (1929, 1934). In one experiment, young *Helix aspersa* of the same size were divided into two groups, one fed on cabbage, oatmeal, and chalk, the other on cabbage and oatmeal alone. One year later, the shells were approximately the same size, but those of animals whose diet included chalk were 4.5 times

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[1] Unfortunately, the size at a whorl criterion has never been used in environmental studies of recent pulmonates. Work has been virtually confined to helicids and other groups with definite adult sizes. Adult size alone has been studied in relation to climatic factors.

as heavy. Other references to the positive correlation of shell thickness with calcium availability include Boycott (1934), Robertson (1941), Schmidt (1955), and Frank and Meyling (1966).

An impressive array of independent phyletic events in *P.* (*Poecilozonites*) points to the conclusion that calcium availability is the controlling factor of shell and callus thickness:

1. *P. nelsoni:* a thin-shelled subspecies lived in red soils; the eolianite subspecies has a thick shell and strong callus.
2. *P. superior:* the shell is thin in *P. s. superior* from the Shore Hills red soil and thick in *P. s. arenicolus* from Harrington-Pembroke eolianites.
3. Shell and callus thickened in the transition from Shore Hills to Harrington and again in the passage from St. George's soil to Southampton eolianite in both eastern and western stocks of *P. bermudensis zonatus* (up to four independent events).
4. The most paedomorphic, and therefore the thinnest shelled, subspecies of *P. bermudensis* evolved in red soils (*P. b. fasolti* and *P. b. bermudensis*).
5. The single eolianite sample of red-soil, thin-shelled *P. n. nelsoni* is thick shelled; the single red-soil sample of eolianite, thick-shelled *P. s. arenicolus* is thin shelled.
6. The most vigorous dune development in Bermuda occurred during Southampton times on the southwest portion of the main island. Shell and callus thickness of *P. b. zonatus* from these eolianites (Sand Quarries, locality 73, and Horseshoe Bay, locality 75) exceed that of all other samples.
7. Modern *P. b. bermudensis* living on exposures of the ancient red soils (Biostation, locality 78, and Perfume Factory, locality 82) have thinner shells than those living on weathered eolianite (Church Ruins, locality 79, and Crawl Point, locality 81).

More intriguing perhaps than the sheer volume of reported instances are the "multiple solutions" utilized by different taxa to obtain the required adaptation: two long-ranging subspecies in *P. nelsoni* and *P. superior*, branching of peripheral isolates by paedomorphosis in *P. bermudensis*, and zigzag fluctuations in the central stock of *P. b. zonatus*.

In conclusion, the effects of temperature cannot be determined. Wetter climates might induce larger and thinner shells. Thin shells will be built when the calcium supply is limited. Since the inferred red-soil environment is colder, wetter, and calcium-poor, the larger size and thinner shells of its snails conform to the expected correlations. The major temporal variations of morphology in the *P. b. zonatus* stock are adaptive in nature.

Oscillating trends in morphology correspond to selective pressures of fluctuating environments, but this observation does not permit an answer to what Mayr and Rosen called "the first question" in their work on geographic variation in *Cerion:* "The first question is to what extent the differences between populations have a genetic basis, or reciprocally to what extent the phenotype of a colony is modified by the effects of the local environment" (Mayr and Rosen, 1956: 42). Limited supplies of calcium evoke selective pressures favoring genetic combinations that produce thin shells, but, as Oldham (1929, 1934) showed, thin shells may also be a simple phenotypic response to lack of building materials; the same adaptive feature may be produced by either route. When morphology alone is available as evidence, it may be impossible to infer the genetic basis of infraspecific variation.

Several guides often employed by paleontologists to distinguish genetic from non-genetic variation are fallacious. McGuire (1966: 895) writes of "nongenetic responses or reversible adaptations to local conditions," but phenotypic results of genetic responses involving general measures of size and shape are readily reversible (Dollo's law, a consequence of probability theory, increases in applicability as structures become complex—

Gould, in press). The absence of definable trends has been taken as an indication of non-genetic variability: "Faunas at each level may be morphologically defined, but few consistently maintained evolutionary trends have been observed. Shell form seems particularly subject to independent, and probably phenotypic variation" (House, 1965: 79); but the complexity of selective pressures in intricately fluctuating environments may produce a pattern of genetically-based variation that seems random. The Bermudian environment approaches the simple model of a two-state oscillation; adaptive morphological responses are similarly uncomplicated.

This inability to distinguish genetic from non-genetic variation has been perceived as a major dilemma by students of pulmonates (Welch, 1958, on geographic variation in *Achatinella;* Rensch, 1932, on the albinism of xerophiles). It has bothered many other evolutionists (Best, 1961, on the spacing of axial tubercles in the trilobite *Encrinurus ornatus;* Mitra, 1958, on basic shape ratios in the brachiopod *Goniorhynchia boueti;* Jolicoeur, 1959, on geographic variation in modern North American wolves; and Nichols, 1962, on local populations of the heart urchin *Echinocardium cordatum* in the British Isles). In each of these instances, morphology was found to be well adapted to a geographic pattern of environmental variation. In *P. b. zonatus*, temporal variation of environments elicits an adaptive response, and I am equally unable to assess the contributions of genetic and non-genetic factors to these adaptations. The extent of morphological alteration is not inconsistent with a purely phenotypic response, but the temporal duration of each successive morphological stage might lead to the implication that some genetic modification is involved. Regardless of the basis of the change, however, oscillations of environment elicit adaptive morphological responses (directly or indirectly); the relationship of climate and morphology in the phyletic history of *P. bermudensis zonatus* is affirmed.

X. INTERSPECIFIC HYBRIDIZATION IN *P. (POECILOZONITES)*

Carlquist (1966: 263) lists the following among his principles of island evolution:

> "Natural hybridization acquires a positive value in evolution of the waif biota."

Cut off from the inflow of new genetic material by oceanic barriers and limited in population size by the area of small islands, extensive interspecific hybridization provides an advantageous mechanism for the dispersion of genetic variability. Maximization of outcrossing is common among plants of waif biotas (Carlquist, 1966).

Interspecific hybridization is fairly common in pulmonates. Cooke (1931) found four hybrid colonies of *Cariella* in boundary zones between species. Lang (1908) described hybrids of *Cepaea nemoralis* and *C. hortensis.* In other cases (Pilsbry, 1912; Mayr and Rosen, 1956), the status of colonies intermediate between two populations is difficult to assess because the taxonomic separation of parental forms has not been adequately ascertained: "The [increased] variability [of intermediate colonies] is either due to true introgression (gene exchange between species) or due to gene flow among well-differentiated allopatric populations of the same species" (Mayr and Rosen, 1956: 1).

Three potential cases of interspecific hybridization, one fairly certain, one probable, and one possible, have been detected between *P. bermudensis* and *P. cupula.*

1. Bus Stop, locality 3: Shore Hills and Harrington snails exposed in a road cut at the first bus stop northwest of Flatts[1] on

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[1] This area is topographically above the upper limit of Devonshire seas. Deposition was continuous throughout the Shore Hills-Harrington interval; the inception of Harrington conditions is indicated by an influx of carbonates diluting the deep red Shore Hills to a pink hue.

TABLE 13. ANALYSIS OF VARIANCE FOR VARIABLES SIGNIFICANT AT 5% LEVEL AMONG THREE GROUPS CONSTRUCTED FROM HYBRID BUS STOP SAMPLE

Variable	F Value	Mean of *bermudensis* Like	Mean of Interme- diate	Mean of *cupula* Like
Relative width of band 2 at 4th whorl	83.81	0.845	0.710	0.430
Relative width of band 2 at 5th whorl	46.19	0.841	0.732	0.498
Relative width of band 3 at 5th whorl	26.80	0.318	0.246	0.221
Initial form index	6.49	0.199	0.242	0.216
Total height plus total width	4.75	28.05	28.29	31.12
Length of aperture	4.45	8.24	8.09	9.06
Height of aperture	3.96	6.36	6.55	7.10
Height at 2nd whorl	3.36	0.937	1.075	1.017

the road to St. George's lack a callus as in *P. cupula* but seem, for the most part, intermediate in shape between *P. bermudensis zonatus* and typical *P. cupula cupula.* A complete and even intergradation in banding pattern from the *cupula* $12^{n}3$ type with sharp band margins to the *zonatus* 123 with diffuse margins is found among the shells of this hybrid population (Pl. 5, figs. 1a–1c).

I selected from the sample three groups of 10 specimens, basing discrimination entirely upon the width and marginal definition of bands 1 and 2. *F* tests were performed on each variable for the three groups (most *cupula*-like, most *zonatus*-like, and intermediate); Table 13 presents a chart of all variables in which significant differences were detected at the 5 per cent level among groups.

The probability of among-group differences in color measures exceeds by a thousand fold that of any size or shape measure. This is, of course, primarily an artifact of the criterion used to define groups, but the reality of far greater color variability can be glimpsed by considering the total observed range of values implied by within-group means. Population variability is average for the highly polygenic characters of size and shape and abnormally high for color measures, which, by analogy to studies of banding in modern pulmonates, have a simple genetic basis. Mayr and Rosen (1956) observed a similar phenomenon in hybrid populations of *Cerion.* "Although hybridization does not necessarily lead to an appreciable increase of phenotypic variability, as shown, for instance, in the case of such highly multifactorial characters as size, there will be an increase in variability for characters with an oligogenic basis. This has in fact been shown in all known cases of hybridization" (Mayr, 1963: 131).

Statistically significant differences in three non-standardized variables (final size, length of aperture and height of aperture) have no biological significance. They are artifacts of the circumstance that four of the measurable *cupula*-like specimens were among the absolutely largest shells of the population (several *zonatus*-like specimens which could not be measured due to protoconch injury are even larger). Significant differences in initial form index and height at the second whorl are referable to a common factor. As expected, early whorl heights of *cupula*-like shells exceed those of *zonatus*-like individuals, but the values for intermediate specimens surpass all others. In his study of interspecific hybrids of *Cepaea nemoralis* and *C. hortensis*, Lang (1908) found that while most characters were intermediate with respect to parental forms, average values for some measures exceeded that of either progenitor.[1]

2. Fort Scaur, locality 69: Abnormally high-spired shells displaying most characteristics of western *P. b. zonatus* are found in a brownish soil of unknown age exposed on the main road at Fort Scaur. (Width/height at fifth whorl = 0.89; lowest for normal *P. b. zonatus* is 1.14. Differential growth ratio and initial form index are 2.44 and .326, respectively, both exceeding any *P. b. zonatus* value.) Although spires of such height are known only in two *P. cupula* subspecies, I would ascribe the Fort Scaur values to convergence were it not for the observation that some specimens of this population exhibit the $02^{n}3$ pattern (Pl. 5, fig. 2), unknown in *P. bermudensis* but found as the most common morph in both high-spired *P. cupula* subspecies (*P. c. dalli* and *P. c. multispira*). (Most Fort Scaur shells have a strong callus and the 023 band pattern.)

3. South Shore local populations of *P. cupula cupula:* These shells, which are "pure" *P. cupula* in the lack of a parietal callus and invariable presence of the $12^{n}3$ band pattern, are unlike typical local populations of *P. cupula cupula* and strikingly similar to *P. bermudensis zonatus* in general measures of size and shape. Although some introgression may be involved, the ascription to convergence of size and shape similarities between these shells and *P. b. zonatus* seems more reasonable, since no color intermediates are known. The most probable case of interspecific hybridization in *Poecilozonites* involves the same local populations and is characterized by complete intergradation of color patterns.

Geographic distribution of the species of *P.* (*Poecilozonites*) is consistent with hypotheses of hybridization. *P. nelsoni* and *P. cupula*, often found in association, never hybridize; *P. cupula* and *P. bermudensis zonatus* had different ecologic preferences, for although their areas of distribution overlap extensively, the two species are never found as such at the same locality. When unusual circumstances brought the two species into direct contact, hybrids seem to have been produced.

In order to assess the relative similarity of proposed hybrids to measured samples of the parental species, a Q-mode factor analysis was performed on the matrix of means of all samples of the two species (Appendix 3). This is a comparison of form alone; all color variables were eliminated, since the identification of hybrids and the discrimination of species is based primarily on color—i.e., we know that color will effect a distinction and wish to discover the diagnostic capacities of a multivariate consideration of form. Numbers 1–36 of Figure 26 represent the same samples (of *P. bermudensis*) as in Figures 17–19 (description in Chapter 8). Numbers 37–57 as follows:

Proposed hybrids:
  1) Bus Stop local population: 57
  2) Fort Scaur local population: 56
  3) South Shore local population of *P. c. cupula:* 37–43
P. cupula:
  4) *P. c. cupula:* Gibbet Island local population: 44
  5) *P. c. cupula:* Whitby local population 45
  6) *P. c. cupula:* Walsingham local population: 46
  7) *P. c. triangularis:* Pink Beach Road local population: 47
  8) *P. c. triangularis:* Devil's Hole local population: 48
  9) *P. c. cupuloides:* Quarry Road local population: 49, 50
  10) *P. c. cupuloides:* Coney Island local population: 51
  11) *P. c. cupuloides:* Bird's Nest local population: 54

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[1] Also relevant to this case is Lang's observation (1908) that the mouth coloring of hybrids was indistinguishable from that of *C. nemoralis*. Absence of a parietal callus (a *P. cupula* feature) in all Bus Stop shells is consistent with the interpretation that they are hybrids.

Figure 26. Plot on varimax axes for all measured samples of *P. cupula* and *P. bermudensis* (see text for explanation). AA stands for 07 and 10, BB for 16, 24, and 36, CC for 31 and 32, DD for 26 and 33, EE for 37 and 41.

12) *P. c. cupuloides:* Surf Bay local population: 55
13) *P. c. multispira:* St. David's Island local population: 52
14) *P. c. dalli:* Albuoy's Point local population: 53.

Sample projections on the first and second axes of a 5-axis solution assume a fairly strong upper left to lower right orientation (Fig. 26), in which several clusters are clearly delineated. (The basically linear orientation is better seen in a 2-axis solution, which still accounts for 95.7 per cent of the total information.) At the lower extreme of the distribution are found the smallest[1] and highest-spired forms (*P. c. dalli* and *P. c. multispira*); at the upper extreme, the largest and lowest-spired (the paedomorphs *P. b. siegmundi*, *P. b. sieglindae*, and *P. b. bermudensis*). When the array is separated into components by construction of lines normal to the trend, the following groups are defined (from lower right to upper left; solid lines separate clusters, dotted lines are arbitrary divisions of a single cluster):

a) (Letters a-g refer to areas marked on Fig. 26). *P. c. dalli,* smallest and highest-spired of all *P.* (*Poecilozonites*).

b) *P. c. multispira,* slightly larger at a whorl, slightly less in spire height. (The fact that *P. c. multispira* attains a large size by uniquely high whorl number does not enter the analysis, since *P. cupula* samples are standardized at $5\frac{3}{8}$ whorls.)

c) All other *P. cupula* with the exception of possible hybrids and the Devil's Hole local population of *P. c. triangularis.*

d) i) *All* proposed hybrids between *P. cupula* and *P. bermudensis.*

ii) Devil's Hole local population of *P. c. triangularis* (lowest-spired of all *P. cupula,* third largest among non-hybrids).

iii) The three *smallest* samples of *P. bermudensis zonatus,* all from the Shore Hills Formation (Nos. 2–4).

e) With the exception of the samples in group d, the smallest *P. bermudensis* populations.

i) The largest Shore Hills *P. bermudensis* population (*P. b. zonatus* from Government Quarry, locality 5).

ii) The lowest-spired Shore Hills *P. bermudensis* population (*P. b. fasolti* from Tom Moore's Caves, locality 53).

iii) The smallest St. George's populations of *P. b. zonatus.*

f) "Normal" *P. bermudensis zonatus.*

i) *All* eolianite samples of *P. b. zonatus.*

ii) The largest St. George's samples of *P. b. zonatus.*

iii) The smallest and highest-spired paedomorphs (5 of 6 samples of modern *P. b. bermudensis*).

g) *P. bermudensis* paedomorphs: All paedomorphic *P. bermudensis* samples with the exception of the *small P. b fasolti* and the *high-spired* modern *P. b. bermudensis.* The single modern sample of *P. b. bermudensis* of this group (Crawl Point, locality 81) is the lowest-spired and next-to-largest of recent forms.

Thus, the standardized measures of size and shape control patterns of relative similarity among samples. The extreme samples are, respectively, the smallest and relatively highest form and the largest and lowest-spired. Progression within the array is completely compatible with this interpretation; no exceptions to the even transition from small, high-spired to large, low-spired forms are found. All proposed hybrids occupy a "buffer zone" in the array of form, separating all *P. cupula* from all *P. bermudensis.*

XI. CONCLUSION

To many medieval thinkers, man was a microcosm of the creation, "the complete abridgement of the whole universe . . . a living emblem and hierogliphick of eternity and time" (Jacob Boehme, quoted in Adams, 1938: 67). Needless to say,

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[1] Smallest in size at a whorl. This is a standardized matrix in which the effects of absolute magnitude are removed.

the Bermudian evolutionary microcosm exhibits not nearly so complete a correspondence to its macrocosm of the total history of life on earth. As I have learned from my work on allometric growth, increase in size is sufficient in itself to expose organisms to new sets of forces requiring new adaptive responses. So foreign to our experience are the forces governing a bacterium's world, that D'Arcy Thompson concluded his famous chapter "On Magnitude" with these words (1942: 77): "The predominant factors are no longer those of our scale; we have come to the edge of a world of which we have no experience, and where all our preconceptions must be recast."

Many phenomena of the Bermudian microcosm represent processes which are important in micro-evolutionary events but of little significance in the long-term phyletic history of major lineages. Random evolutionary change—the proposed initiation of infraspecific diversity in *P. cupula* according to the founder principle—does not produce the adaptive and progressive changes in form that characterize the evolutionary history of higher taxa. In another example, morphological adaptations in the phyletic history of *P. b. zonatus* may be purely phenotypic; trends involving much longer time spans and more profound alterations of form will always have a genetic basis. In more general terms, micro-evolutionary studies focus on the production of diversity in response to isolation and environmental differences. The extrapolation of these emphases leads to a "species divergence model," which views the evolution of higher taxa as a simple extension of microcosmic processes of speciation—i.e., the higher taxon is viewed as a larger branch on the traditional tree, the boughs and branches of which continually diverge. This extrapolation does not give sufficient emphasis to the massive parallelism and trends toward increased mechanical efficiency that proceed in a relatively constant physical environment. These are major determinants of patterns in transspecific evolution but have little relevance to phenomena of infraspecific variation.

In spite of this, the microcosm is a proper place to begin, for only here can the variables be sufficiently limited to permit an unambiguous tracing of actual evolutionary histories rather than possible structural sequences (which always involve the application of *a priori* hypotheses concerning the most probable routes of evolutionary change). Moreover, some aspects of the history of *Poecilozonites*—in particular, the four-fold iterative paedomorphosis of *P. bermudensis*—involve the repetitive occurrence of adaptive events, an outstanding feature of the macrocosm not often recorded at the level of infraspecific diversity. These repetitive events have a special importance in paleontology that is not often realized. Paleontology, when it deals with the documentation of phylogeny, operates in the realm of history. Simpson notes that "historical events are unique, usually to a high degree, and hence cannot embody laws defined as recurrent repeatable relationships" (1963: 29). But history becomes scientific when inductive generalizations are derived from series of events by the extraction of repetitive aspects from their integral uniqueness. By establishing a role for induction in history, repetitive occurrence leads to the formulation of laws; this is the major contribution of parallelism, convergence, and iteration to the explanation of evolutionary events—for explanation involves subsumption of observed conditions under general laws. As Harris and Morren (1966: 127) have noted for the related field of sociocultural evolution: "Convergences and parallelisms . . . are the prime source of evidence for the existence of regular and lawful selective processes in sociocultural evolution. In them reside the chief natural substitute for laboratory controls and the greatest hope for the formulation of operationally valid theories of sociocultural causation."

To obtain the detail required for unambiguous documentation of evolutionary events, we sacrifice the extensive time, geography and morphological change of major chapters in the history of life. An expert, it is said, is one who knows more and more about less and less. Our hope, however, is that such limitation will enable us to establish general principles which, although undiscoverable in the "more and more" of space, time, and morphology, are applicable to it.

XII. SUMMARY OF ARGUMENTS

1. Introduction

1a. The extreme limitation of time and space attained in studying the Bermudian Pleistocene eliminates many confusing variables that usually hinder evolutionary interpretations.

1b. If the operation of evolutionary processes in time is the object of study, chronologic placement of a time segment is of no special importance. The Pleistocene presents several advantages based on good preservation and usual persistence of species in the modern fauna.

1c. Previous studies of Pleistocene pulmonates have failed to provide evidence for evolutionary events other than extinction. This is probably an artifact of confining studies to the specific level. Infraspecific patterns of variation must be considered.

2. Geologic and Biological Background

2a. The stratigraphic column of Pleistocene Bermuda is an alternating sequence of interglacial carbonates (dunes and shallow water limestones) and glacial red soils. Snails are most common in red soils and unindurated zones of the eolianites.

2b. At the peak of its Pleistocene diversity, *Poecilozonites* contained three subgenera and 15 species varying from 5–45 mm in width and occupying a broad range of ecologic roles—a classic case of insular divergence after chance introduction to an area free from competitors. High stands of interglacial seas and the later introduction of pigs, rats, and other pulmonates by man have reduced this diversity drastically.

2c. This study deals with all taxa of one of the three subgenera—*P.* (*Poecilozonites*).

3. Quantification

3a. There are two major roles for quantitative data in this study: i) Comparisons among variables: Redundancies can be eliminated and the causal factors of association among variables (in ontogeny and phylogeny) inferred.

ii) Comparisons among samples: Since allometry is so pervasive in the ontogeny of these pulmonates, samples can be properly compared only when all the variables characterizing them have been standardized at a common size or whorl number. The standardized "matrix of means" provides the data for objective multivariate comparisons among variables.

3b. Forty-four raw and derived variables are defined, including measures of color and thickness, as well as those of size and external shape. These allow a fairly complete reconstruction of the shell from their values alone and should encompass the significant dimensions of metric variability.

4. Ontogeny of P. (Poecilozonites)

4a. The ontogenetic relationship between each variable and shell size is allometric.

4b. Ontogeny of color: Intensity of coloration increases with growth as the intermittent blotches of early ontogeny coalesce to form a band and the bands increase in relative width.

4c. Ontogeny of shape: Allometric trends in shape are determined by several factors and may be complex. The protoconch is a nucleus about which the early whorls must be molded. The primary control of later growth is exerted by doming of the spire, largely produced by increasing relative height of the aperture.

5. Interrelationship of Variables

5a. The interrelationship of variables is approached by factor analysis, which discerns clusters of variables by the projection of their vectors onto a small number of reference axes.

5b. The following clusters were obtained in an 8-axis solution for a *P. bermudensis* sample from locality 5 (25 specimens, 45 variables, size range 23.2–37.8 mm): size (most non-standardized raw variables), form ratio, standardized widths and heights, color.

5c. Successive reduction of factor axes produces a hierarchy of relative size independence. More and more variables are incorporated into the size cluster (even standardized widths are weakly related to size) until, in a 2-axis solution, only standardized heights retain their separate sorting.

5d. Ten other analyses yield similar results. The smaller the size range of the sample, the weaker the controlling influence of absolute size upon variable interrelationships. Several variables are redundant: total width at the first whorl, for example, is always tied to protoconch width.

6. Evolution of P. cupula

6a. Three species of previous authors and two forms that would have merited specific status under criteria previously used are constituted as subspecies of *P. cupula.* Each occupies a unique segment of the species' geographic range and has a non-disjunct temporal distribution—thus satisfying criteria for a biological subspecies. In particularly favorable cases, the biospecies is an operational concept in paleontology.

6b. *P. c. cupula,* largest among *P. cupula* at the fifth whorl, probably evolved from *P. c. cupuloides* by stabilization of one morph of the latter's four-fold polymorphism. In polymorphic *P. c. cupuloides,* shells of this morph are significantly larger than those of others. Moreover, shells of *P. c. cupuloides* from populations which have stabilized the three other morphs are smaller than those of *P. c. cupula* or of the *cupula*-like morph of *P. c. cupuloides.* This pervasive correlation of color and size suggests that color variation, often so difficult to interpret in adaptive terms, may be a pleiotropic concomitant of other selected characters.

6c. The diversity of *P. cupula* can be related to sea level changes in the Pleistocene history of Bermuda. The main period of diversification (three new subspecies) is coincident with a high sea stand (plus five meters) that dissected Bermuda into a large number of isolated islands; the extinction of the species (four subspecies) is related to a higher sea (plus 20 meters), that virtually inundated the entire land mass.

6d. The role of random evolutionary factors (genetic drift and the founder principle) has been the focus of a major debate among pulmonate specialists. The demonstration that selection *could* serve as a completely sufficient cause of differences among populations need not prove that it *does* so serve. The reduced color variability of one or a few chance founders probably played a role in the stabilization of morphs in post-Walsingham populations of *P. c. cupuloides.*

7. Evolution of the P. nelsoni Stock

7a. Of five subspecific names available in the typological compendium of shapes that formed the previous classification of *P. nelsoni,* four fail to meet criteria for biological subspecies. All four occur in red soils, but their sporadic distribution in space and lack of morphological distinctness suggests one single, highly variable taxon—*P. n. nelsoni.*

7b. The fifth, *P. n. callosus,* is smaller, more weakly colored and thicker shelled than *P. n. nelsoni.* Moreover, it has a distinct geographic distribution, being confined to eolianites.

7c. In two red-soil localities, a closely related form is found with *P. n. nelsoni.* This is a new species (presumed sympatry without interbreeding)—*P. superior superior.* This species also has a thicker-shelled and more weakly-colored eolianite counterpart, *P. s. arenicolus.* The *P. nelsoni* stock is composed of two species, each with a red-soil and an eolianite subspecies.

7d. The eolianite subspecies of both species share common features, independently developed of course, which can be interpreted in adaptive terms. The thick shell is related to the availability of lime, while weaker coloration, as Rensch has suggested, may better reflect sunlight in the highly illuminated white dune environment, or may serve a cryptic function.

7e. The vertical sequence *nelsoni-callosus-nelsoni* (Shore Hills red soil, Harrington-Pembroke eolianite, St. George's red soil) does not represent zig-zag evolution, but rather the incomplete record of two subspecies tied to environments that migrated back and forth over the Bermuda platform in response to shifting sea levels of the glacial period.

8. *Phyletic Branching in* P. bermudensis

8a. Paedomorphic populations of *P. bermudensis* are found in four distinct spatiotemporal regions of Pleistocene Bermuda. They are essentially scaled-up replicas of juvenile shells of the central stock, *P. b. zonatus* (Pl. 4, figs. 1–6).

8b. Each of these four populations represents an independent episode of paedomorphosis.

8c. Each paedomorph is a distinct genetic entity, not a mere phenotypic response to a recurrent set of environmental conditions. Each paedomorph has the geographic distribution of a peripheral isolate, and each has lost genes for previously adult features that could never be brought to phenotypic expression.

8d. Paedomorphosis has occurred by a prolongation of rapid juvenile growth rates to later sizes.

8e. The most intense episodes of paedomorphosis occurred in red soils, less intense in unindurated zones and none in carbonate dunes. Paedomorphosis is one pathway (of several taken by various *Poecilozonites* taxa) to the development of thin shells in the low calcium environment of red soils.

9. *Phyletic Evolution of* P. bermudensis zonatus

9a. The relationship of form and environment in pulmonates has been a subject of debate since Darwin's time. For reasons related both to their ideas of evolution and their larger world view, Gulick and Crampton denied the environment a major role, but the modern evolutionary synthesis has reasserted the importance of environment in setting the direction of natural selection.

9b. The Bermudian stratigraphic sequence reflects a two-stage oscillation of glacial (red soil) and interglacial (marine and dune carbonate) conditions. Zig-zag trends in the morphology of *P. b. zonatus* correspond to the alternation of environments (Figs. 23, 24). Shells are thin and small-at-a-whorl in red soils, thick and large-at-a-whorl in eolianites.

9c. These trends are the same as those noted for modern pulmonates in a similar range of environments. The trends are clearly adaptive. Particularly strong is the correlation of shell thickness and availability of lime for seven independent events in several taxa of *P.* (*Poecilozonites*).

9d. It is one of the frustrations of such work that, while we can affirm the adaptive nature of a correlation between climate and morphology, we cannot tell whether we are dealing with genetically determined changes or purely phenotypic responses.

10. *Interspecific Hybridization:* P. cupula-P. bermudensis

10a. *P. cupula* and *P. bermudensis,* although sympatric, apparently did not occupy the same habitat. When brought into direct contact, the two species hybridized. Two populations, intermediate in form and exhibiting the complete color range from "pure" *cupula* to "pure" *bermudensis* are interpreted as hybrids (Pl. 5).

10b. Two varimax factor axes account for 95.7 per cent of all information of all samples of the two species. The 57 samples (each based on 25 standardized variables) are arranged in roughly linear order varying from the smallest and highest-spired form (*P. cupula dalli*) to the largest and lowest-spired (*P. bermudensis* paedomorphs). No exceptions to the even transition from one extreme to the other are found within the array. All hybrids occupy a "buffer zone" separating all *P. cupula* from all *P. bermudensis.*

NOTES ADDED IN PROOF

Since this work was written and processed at the pace traditionally identified with its zoological subject, I hasten to add some new information of the last two years:

1. The correlation of wide protoconch, intense coloration and height of later whorls, noted and puzzled over in Chapter 5, has now been affirmed for two species of the subgenus *P.* (*Gastrelasmus*). G. Edynak, working with my assistance but without my prompting (as I had quite forgotten about the result), obtained R-mode clusters of protoconch width, late heights and color flame widths in both *P. blandi heilprini* and *P. reinianus vanattai* (Shore Hills Soil, Prospero's Cave). An intensified developmental (metabolic?) rate might produce all these features—large protoconchs (in large eggs), strong doming, and more complete coverage of the shell surface with color flames.

2. An inference that I termed "very speculative" and "tenuous" turns out to be false. *P. cupula triangularis* did not arise at the base of the Harrington. I have now found it in a Walsingham unindurated zone on the Air Base and in the Shore Hills soil in the city of Hamilton.

3. The morphologic oscillations of *P. b. zonatus* in western Bermuda, shown in Figures 23 and 24, were not well established because the St. George's points were based upon one sample only. I have since found another exposure of St. George's soil at the south end of Ireland Island and am pleased to report that 10 specimens yield an average value of .126 mm for callus thickness and 14.52 mm for size at fifth whorl. Both are much smaller than any comparable value for any eolianite sample of *P. b. zonatus.*

4. A study of microgastropod form and frequency (to be published in the proceedings of the 1969 North American Paleontological Convention) has elucidated some reasons for the ecological separation of *P. bermudensis* from *P. cupula* and *P. nelsoni* and for the extinction of the latter two. *P. cupula* and *P. nelsoni* are not found with gastropod assemblages that indicate warmth and dryness, just those conditions associated with the high Spencer's Point sea that heralded their demise.

5. The microgastropod study has provided several more correlations of form and diversity with Pleistocene climates. *Thysanophora hypolepta* and *Carychium bermudense* display oscillating trends in morphology, but their adaptive significance is unclear. Availability of $CaCO_3$ is again a controlling factor. The non-calciphilic *Thysanophora hypolepta* dominates red soil samples, but calciphilic species of *Gastrocopta*, *Carychium*, and *Vertigo* dilute its relative abundance in eolianites.

6. I have located the type of *P. cupula dalli*, mixed among related material in the collections of the United States National Museum, Washington, D.C. It has been recatalogued and given the number U.S.N.M. 679536 (Division of Mollusks). Its coloration ($02^{n}3$) and form clearly ally it with the Albuoy's Point sample, but the more angulate periphery and higher spire (though, I suspect, not a stronger dome) are beyond the variability range of Albuoy's Point and suggest a separate local population of *P. c. dalli.* Moreover, the matrix indicates a red soil cave filling (and therefore almost surely Shore Hills—I know of no St. George's cave deposits that have yielded fossils). This

finding removes the somewhat disturbing datum that *P. c. dalli* had been the only taxon of *Poecilozonites* known from a single locality. But it also invalidates (along with the new *P. c. triangularis* data of this addendum) my tenuous inference associating origin of several subspecies with the Devonshire sea stand. However, my firmer conclusion, that all subspecies were extinguished during the Spencer's Point high sea stand, has been strengthened by the discovery of many new St. George's and Southampton localities, none of which contain a trace of *P. cupula*.

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Appendix I:

SYSTEMATICS

These skeleton descriptions contain only the basic information of type repository and locality, morphology, and distribution. The details of morphological distinction are summarized in the matrices of means, Appendix 3.

Class: Gastropoda

Subclass: Pulmonata

Order: Stylommatophora

Family: Zonitidae

Subfamily: Poecilozonitinae Pilsbry, 1924

Genus: *Poecilozonites* O. Boettger, 1884

Type: *Helix bermudensis* Pfeiffer, 1845, designated by Pilsbry, 1888: 286

Subgenus: *Poecilozonites* (*Poecilozonites*) Pilsbry, 1924

Poecilozonites bermudensis (Pfeiffer, 1845)

Type: *Poecilozonites bermudensis bermudensis* (Pfeiffer, 1845)[1]

Diagnosis: Shell generally larger, lower-spired, and less intensely domed than in *P. cupula;* smaller and more strongly-domed than *P. nelsoni;* coloration pattern 123 in eastern Bermuda (eastern Devonshire Parish and eastward) and 023 in western Bermuda during Shore Hills to Southampton times; recent shells all 123; band margins diffuse in 123 form, fairly sharp in 023 shells; supplementary color wash usually present below band 3; relative width of band 3 invariably greater than in *P. cupula;* "faded" variation (bands replaced during ontogeny by lines at the band peripheries) present in all 123 samples save *P. b. fasolti* and *P. b. bermudensis;* parietal callus present in *P. b. zonatus*, *P. b. siegmundi*, and *P. b. sieglindae;* strongly angulate at periphery of the fifth whorl.

Distribution: Island-wide. Shore Hills-Recent.

Poecilozonites bermudensis zonatus Verrill, 1902

Plate 4, nos. 1 and 2. M.C.Z. Nos. 28987 and 28988

Poecilozonites bermudensis zonata—Verrill, 1902, Trans. Conn. Acad. Arts Sci., v. 11, p. 728 (footnote; no figure). Formally described in Verrill, 1905, Trans. Conn. Acad. Arts Sci., v. 12, pp. 164 and 191 as (emend.) *Poecilozonites bermudensis zonatus*. Holotype and paratypes figured in Verrill, 1905, plate 27, figure 2. Localities not specified; both eastern and western snails are figured. I have not been able to locate the actual type specimens.

Description: Color pattern is 123 in eastern Bermuda, 023 in western Bermuda; generally, all bands have formed by the fifth whorl; highest-spired, most strongly-domed and relatively highest of *P. bermudensis* subspecies; umbilicus relatively narrow for the species; parietal callus well developed; aperture relatively high and

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[1] Repository of types not specified. The identity, based on illustrations of Pfeiffer's shells in Reeve (1854), is beyond doubt.

rounded in outline; size at fifth whorl spans entire range for species; 5 1/4 to 6 2/4 postprotoconch whorls at maximum (only Shore Hills samples exceed 6 whorls).

Distribution: Island-wide. Shore Hills-Southampton.

Poecilozonites bermudensis fasolti new subspecies

Holotype: Plate 4, no. 3. M.C.Z. No. 28989

Holotype from locality 53, Tom Moore's Caves, Hamilton Parish, Shore Hills Soil.

Description: Color pattern 1^f2^f3; flame-band transition occurs after fifth whorl and is rarely seen at all; spire very low and weakly domed, making *P. b. fasolti* the relatively widest subspecies of *P. bermudensis;* umbilical width maximum for species; parietal callus never developed; aperture relatively high (though lower than Shore Hills *P. b. zonatus*), with angular outlines; small at fifth whorl, as in all Shore Hills *P. bermudensis:* 6 postprotoconch whorls at maximum.

Remarks: Paedomorphic offshoot of Shore Hills *P. b. zonatus.*

Distribution: Known from a single locality, Tom Moore's Cave, Hamilton Parish. Shore Hills Soil.

Poecilozonites bermudensis siegmundi new subspecies

Holotype: Plate 4, no. 4. M.C.Z. No. 28990

Holotype from locality 10, southern tip of Ireland Island, Sandys Parish, Harrington Formation.

Description: Color pattern 023, with band formation occurring later in ontogeny than in typical western *P. b. zonatus;* spire low and weakly domed but relatively highest among the paedomorphic subspecies of *P. bermudensis;* umbilicus moderately wide; parietal callus weakly developed; aperture relatively low with angular outline; large at fifth whorl; 5 to $5\frac{6}{8}$ postprotoconch whorls at maximum.

Remarks: Paedomorphic offshoot of western *P. b. zonatus.*

Distribution: Southern end of Ireland Island, Sandys Parish, Harrington Formation.

Poecilozonites bermudensis sieglindae new subspecies

Holotype: Plate 3, no. 5, M.C.Z. No. 28991

Holotype from locality 44, Rocky Bay, Devonshire Parish, Harrington Formation.

Description: Color pattern 123, with band formation occurring later in ontogeny than in typical eastern *P. b. zonatus;* spire low and weakly domed; umbilicus wide; parietal callus weakly developed; aperture relatively low with angular outline; large at fifth whorl; 5 to $5\frac{6}{8}$ postprotoconch whorls at maximum.

Remarks: Paedomorphic offshoot of eastern *P. b. zonatus.*

Distribution: Rocky Bay, Devonshire Parish, Harrington-Pembroke Formations.

Poecilozonites bermudensis bermudensis (Pfeiffer, 1845)

Plate 4, no. 6. M.C.Z. No. 28992

Helix bermudensis—Pfeiffer, 1845, Proc. Zool. Soc. London, v. 13, p. 67. (Complete synonymy up to 1889 given in Pilsbry, 1889a. Inclusion in *Poecilozonites* has not been questioned since then.) Pfeiffer's description lists habitat simply as "Bermuda"; no figure given. Pfeiffer's shells are figured by Reeve, 1854, plate 57. They are Recent forms.

Description: Color pattern 1^f2^f3 in St. George's-Southampton forms, often 123 in Recent shells; spire weakly domed in all forms, low in St. George's-Southampton, moderate to high in Recent forms due to increase in early whorl heights; umbilicus wide in St. George's-Southampton, moderately wide in Recent samples; callus not developed; large at fifth whorl in St. George's-Southampton, small to moderate in Recent; 5 to $5\frac{1}{2}$ postprotoconch whorls at maximum.

Remarks: Paedomorphic offshoot of eastern *P. b. zonatus.*

Distribution: Confined to St. George's Island, St. George's Parish in St. George's-Southampton times. Island-wide at present.

Poecilozonites nelsoni (Bland, 1875)

Type: *Poecilozonites nelsoni nelsoni* (Bland, 1875)

Diagnosis: Shell larger, dome more triangular in cross section than other taxa of subgenus; color pattern 123 or 023; parietal callus weakly developed in red soils, strong in eolianites; 7 to 8 postprotoconch whorls in large specimens; distinguished from *P. cupula* and *P. bermudensis* by larger size, whorl number, and weakly-domed spire and from *P. superior* by lower spire, weaker dome, and strength of second color band.

Distribution: Shore Hills-St. George's. Island-wide.

Poecilozonites nelsoni nelsoni (Bland, 1875)

Plate 2, nos. 1–7

Hyalina nelsoni Bland, 1875, Ann. Lyceum Nat. Hist. New York, vol 11, p. 78. Locality listed as "Bermuda," repository of types unspecified.

Poecilozonites nelsoni var. *discoides* Gulick, 1904, Proc. Acad. Nat. Sci. Phila., p. 416. Locality listed as "large quarry 1/2 way bet. Tuckerstown and Walsingham." Shore Hills soil. Holotype: Plate 2, no. 1 (A.N.S.P. No. 58084).

Poecilozonites nelsoni conoides Verrill, 1905, Trans. Conn. Acad. Arts Sci., p. 163. Locality listed as "near the western shore of Castle Harbour in a mass of red-clay and stalagmite," Shore Hills soil. Topotype: Plate 2, no. 4 (M.C.Z. No. 29013).

Description: Color pattern 123 with diffuse band margins (023 with sharper margins in Shore Hills samples from Sandys Parish); spire low (Gulick's rejected *P. n. discoides*) to high (Verrill's rejected *P. n. conoides*); rather triangular in cross section; protoconch and size at fifth whorl largest for subgenus; maximal size (77.6 mm) and postprotoconch whorl number (8) for subgenus; callus absent or weakly developed; umbilicus relatively wide in most samples; rounded to angulate at fifth whorl periphery.

Distribution: Shore Hills-St. George's. Island-wide in Shore Hills, Smiths Parish in Harrington-Pembroke, Hamilton and St. George's Parish in St. George's.

Poecilozonites nelsoni callosus Gulick, 1904

Plate 3, nos. 1–3

Poecilozonites nelsoni var. *callosus* Gulick, 1904, Proc. Acad. Nat. Sci. Phila., p. 416. Locality listed as "Benj. Trott's sand pit Tucker's Town," from unindurated zone presumably Harrington in age. Holotype: Plate 3, no. 2 (A.N.S.P. No. 58086).

Description: Color pattern 023 with sharp band margins; spire medium in height, rather triangular in cross section; smaller than *P. n. nelsoni* in maximal size, whorl number, protoconch width, and size at fifth whorl; shell thick with strongly developed parietal callus; umbilicus usually constricted by shell thickening; angulate at periphery of fifth whorl.

Distribution: Harrington-Pembroke in eastern Bermuda.

Poecilozonites cupula Gulick, 1904

Type: *Poecilozonites cupula cupula* (Gulick, 1904)

Diagnosis: Shell generally smaller and higher-spired than other members of subgenus; distinguished from *P. bermudensis* by following features of coloration: different banding patterns ($12^{n}3$, $1^{f}00$, $1^{f}03$, $02^{n}3$, $1^{f}2^{n}3$), sharpness of band margins, absence of a supplementary color wash below band 3, lower relative width of band 3, and absence of the "faded" variation; differs from *P. nelsoni* and *P. superior* by smaller size and generally stronger dome; parietal callus lacking in all subspecies; faintly to moderately angular at periphery of the fifth whorl.

Distribution: Walsingham-Pembroke in eastern Bermuda. No specimens known west of Devonshire Bay with exception of possible hybrid population at Fort Scaur, locality 69.

Poecilozonites cupula cupula (Gulick, 1904)

Plate 1, no. 1. M.C.Z. No. 29006

Poecilozonites cupula—Gulick, 1904, Proc.

Acad. Nat. Sci. Phila., v. 56, p. 417. Holotype, A.N.S.P. No. 58085, Department of Malacology. Locality described as "large quarry 1/2 way between Tuckerstown and Walsingham. A. Gulick, 1903!" Paratypes bear No. A.N.S.P. 85507. Shore Hills Soil.

Description: Color pattern invariably 12^n3; spire high and strongly domed (type locality, Walsingham local population) to low and moderately domed (South Shore local population); protoconch and size at fifth whorl largest among *P. cupula* subspecies; 5½ to 6½ postprotoconch whorls at maximum.

Distribution: Hamilton, Smiths, and southeast corner of Devonshire Parishes, Shore Hills-Pembroke.

Poecilozonites cupula dalli (Gulick, 1904)

Plate 1, no. 2. M.C.Z. No. 29007

Poecilozonites dalli—Gulick, 1904, Proc. Acad. Nat. Sci. Phila., 56: 417. Type locality unknown, repository of type unspecified. Figure and description agree entirely with Albuoy's Point sample described below.

Description: Polymorphic in color; morphs 1^f03, 02^n3 and 1^f2^n3 are known, of which the second predominates; highest and most strongly-domed spire of all samples of *Poecilozonites;* smallest protoconch and size at fifth whorl and absolutely smallest form of subgenus; umbilicus constricted due to increased intensity of doming during ontogeny; aperture relatively high and narrow; 5½ to 6 postprotoconch whorls at maximum.

Distribution: Known from a single locality, Albuoy's Point, Smiths Parish (locality 4), Harrington-Pembroke (?).

Poecilozonites cupula cupuloides (Peile, 1924)

Plate 1, no. 3. M.C.Z. No. 29008

Poecilozonites cupuloides—Peile, 1924, Proc. Malacol. Soc. London, 16: 17. Holotype in British Museum. Paratypes at Philadelphia Academy of Natural Sciences, A.N.S.P. No. 131584, Department of Malacology, labeled "'cupuloides' (part of original lot) 80 yds. N. of Harrington House, Harrington Sd. Base of 10 ft. hard limestone road cutting. Arthur Haycock 1922!" Walsingham Formation. Holotype displays morph 1^f2^n3.

Description: Polymorphic in color, morphs 1^f00, 1^f03, 02^n3 and 1^f2^n3; all four present in oldest Quarry Road local population, first and second stabilized in Coney Island local population, the third in Bird's Nest and Surf Bay local populations. Spire moderate in height and doming intensity; size at fifth whorl and maximal size moderate for the species; 5¾ to 6¼ postprotoconch whorls at maximum.

Distribution: Hamilton Parish, Tucker's Town, Walsingham-Shore Hills.

Poecilozonites cupula multispira new subspecies

Holotype: Plate 1, no. 4. M.C.Z. No. 29009

Holotype from locality 84, St. David's Island, St. George's Parish. Largest specimen of the sample. Harrington-Pembroke (?).

Description: Polymorphic in color; morphs 02^n3 and 1^f2^n3 are known, of which the former predominates; spire of large specimens high, but only moderately domed; strong relative height attained by addition of whorls (a large specimen may have 8 postprotoconch whorls); although maximal size is largest among *P. cupula* subspecies, size at the fifth whorl exceeds that of *P. c. dalli* only slightly (and insignificantly); 7 to 8 postprotoconch whorls at maximum.

Distribution: St. David's Island, St. George's Parish, Harrington-Pembroke (?).

Poecilozonites cupula triangularis new subspecies

Holotype: Plate 1, no. 5. M.C.Z. No. 29010

Holotype from locality 46, South Shore Road at Pink Beach, southeast corner of Smith's Parish. Pembroke Formation.

Description: Polymorphic in color; morphs 02^n3 and 1^f2^n3 are present; lowest spire, least strongly-domed and relatively widest subspecies of *P. cupula;* as relatively widest form, fairly angulate at periphery (other subspecies of *P. cupula* very weakly carinate), but peripheral keel still not as strong as in more strongly domed *P. bermudensis;* size at fifth whorl exceeded only by *P. cupula cupula*; 5 to $5\frac{6}{8}$ postprotoconch whorls at maximum.

Poecilozonites superior new species

Type: *Poecilozonites superior superior* new subspecies

Diagnosis: Shell large and strongly domed with high spire; color 123 with sharp band margins, $12^{n}3$ or 103; parietal callus absent or weakly developed even when shell thick; 7 to 8 postprotoconch whorls in large specimens; distinguished from *P. bermudensis* by color and larger size and whorl number, from *P. cupula* by larger size and whorl number, from *P. nelsoni* by color, higher spire, and stronger dome.

Distribution: Shore Hills-Pembroke, eastern Bermuda.

Poecilozonites superior superior new subspecies

Holotype: Plate 2, no. 8. M.C.Z. No. 29016

Holotype from locality 5, Government Quarry (Bird Fissure), Shore Hills Soil.

Description: Color pattern 123 with sharp band margins; spire high and strongly domed in cross section; smaller and fewer whorls at final size than in *P. nelsoni*; shell thin; callus absent or weakly developed; umbilicus constricted by increase in spire height in ontogeny; rounded at fifth whorl periphery.

Distribution: Shore Hills, Hamilton Parish.

Poecilozonites superior arenicolus new subspecies

Holotype: Plate 3, no. 4. M.C.Z. No. 29019

Holotype from locality 11, Ferry Road north of Biostation, Pembroke eolianite.

Description: Color pattern $12^{n}3$ or 103; spire high and strongly domed in cross section; protoconch generally smaller than in *P. n. nelsoni* or *P. s. superior;* shell thick but callus still absent or weakly developed; umbilicus constricted by spire height and shell thickening; faintly angulate to rounded at fifth whorl periphery; up to 8 whorls at final size.

Distribution: Shore Hills to Pembroke, eastern Bermuda.

Appendix 2:

REGISTER OF LOCALITIES

Localities are described in numerical order. Following the descriptions, locality numbers are listed by parish and by subspecies. Only localities mentioned in the text are described. I shall be glad to furnish a more detailed list to any enquirer.

1. Northern end of Whalebone Bay. Harrington unindurated zone, averaging two feet in thickness, overlies Devonshire sands and veneer of intertidal conglomerate. Shore Hills soil stripped away for the most part, but preserved in "palmetto stumps," solution pipes in the massive Belmont marine limestone. Snails from Harrington and base of overlying Pembroke eolianites.

2. South shore on promontory west of Devonshire Bay. Harrington unindurated zone overlies well-developed Devonshire intertidal marine conglomerate covering massive Belmont marine limestone. Leeward beds of a Pembroke dune overlie Harrington.

3. North Shore Road, first bus stop northwest of Flatts on road to St. George's. North side of road. A one-foot thick exposure of Shore Hills soil is overlain by a foot of pinkish Harrington deposition. No intervening Devonshire, since area is topographically above maximum extent of Devonshire sea. Hybrids of *P. c. cupula* and *P. b. zonatus*.

4. Albuoy's Point, road cut north of

South Shore Road. *P. c. dalli* in unindurated zone.

5. Government Quarry. Numerous fissures in Walsingham eolianite filled with Shore Hills soil. Each fissure has a distinct fauna; they are almost surely of different ages. *P. b. zonatus* in Graveyard Fissure (mostly quarried away by 1967), *P. n. nelsoni* and *P. b. zonatus* in Main Fissure (south wall of quarry), *P. n. nelsoni* and *P. s. superior* in Bird Fissure (quarried away), and *P. n. nelsoni* in Coquina Fissure (west wall).

6. Black Watch Pass. *P. b. zonatus* in unindurated zone (Harrington or Pembroke) at the base of the road cut at the north end of Black Watch Pass. Zone rises to south.

9.[1] Harrington Sound Road at northern entrance to Government Quarry. *P. c. cupuloides* in poorly-developed intra-Walsingham red soil exposed on erosional high, and in Walsingham eolianite above. A single *P. n. nelsoni* or *P. s. superior* from a Shore Hills-filled Walsingham fissure.

10. Southern tip of Ireland Island. Type locality of *P. b. siegmundi*. Poorly-developed Harrington unindurated zone overlies Devonshire eolianite that can be traced to typical Devonshire intertidal conglomerate on the northwest coast.

11. Ferry Road, north of Biostation. Thin deposits of Shore Hills and St. George's soils with Pembroke eolianite between. *P. s. arenicolus* in Shore Hills and Pembroke; *P. b. bermudensis* in overlying Southampton eolianite.

12. Mullett Bay Road. St. George's soil on erosional high exposed for 10 meters along the road, diving beneath road level at each extremity of the outcrop. A few *P. b. bermudensis*.

15. Sand pit in golf course of St. George's Hotel. An unindurated zone in Southampton eolianite. Type locality for Sayles's (1931) rejected "McGall's soil."

16. Mullett Bay Road just before entrance to St. George's Towne. Good development of St. George's soil on erosional high. Type St. George's with a few *P. b. bermudensis*.

17. Abandoned railroad cut east of Whalebone Bay. Good exposure of Pembroke and Southampton eolianites with strong St. George's profile (1/2 to 3 feet thick). *P. b. zonatus* in St. George's and at several levels in the Southampton.

18. Abandoned railroad cut west of Tank Farm Pier. *P. n. nelsoni* in St. George's soil, filling fissure in Pembroke eolianite.

21. Quarry cut between Mullet Bay Road and abandoned railroad cut exposing Southampton dune. *P. b. bermudensis* found at three levels: in, above (eolianite), and below (eolianite) a brownish unindurated zone. Lower eolianite is locality 21a; upper is 21d.

24. Khyber Pass, Signal Hill. Unindurated zone (averaging 3 feet in thickness) in a Southampton dune. Type locality of Sayles's (1931) rejected "Signal Hill Soil."

27. Tobacco Bay. *P. b. bermudensis* in loosely-consolidated Southampton eolianite.

28. East coast of St. George's Island at Buildings Bay. Good development of Harrington Formation containing only known shells of *P. b. zonatus* on St. George's Island.

30. North Shore Road at "Bird's Nest" residence. Well-developed profile of Shore Hills soil dips westward. *P. c. cupuloides* in Belmont eolianite just below the base of the Shore Hills. *P. nelsoni* in both Shore Hills (*P. n. nelsoni*) and unindurated zone of overlying (Pembroke?) eolianite (*P. n. callosus*). Only known locality in which *P. nelsoni* is found in two superposed horizons.

31. South shore, west end of Spittal Pond. St. George's soil on erosional high

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[1] Missing numbers correspond to collecting localities that either yielded no *Poecilozonites* or provided specimens not discussed herein.

atop Pembroke dune covering Shore Hills deposits.

32. South shore, east of Spanish Rock. Unindurated zone in Pembroke dune.

34. Wilkinson's Quarry. Very strong development of Shore Hills soil. *P. n. nelsoni* in several Shore Hills fissures within Walsingham eolianite. One fissure (south wall) has both *P. n. nelsoni* and *P. s. superior.*

35. South shore at deep inlet east of Spencer's Point. Unindurated zone in Pembroke dune, may be correlative with locality 32. *P. c. cupula.*

36. Quarry south of South Road, north of Spencer's Point. *P. b. zonatus* in massive, poorly-consolidated upper Southampton eolianite.

37. South shore, western end of McGall's Bay. *P. b. zonatus* in thin layer of St. George's soil overlying Spencer's Point intertidal marine conglomerate.

39. South shore at eastern end of Saucos Hill. *P. c. cupula* in whitish well-developed unindurated zone and in overlying eolianites. Harrington-Pembroke interval.

40. North slope of Saucos Hill south of South Road. *P. b. zonatus* in barely consolidated late Southampton eolianite.

41. South shore at western end of Saucos Hill. Most complete superposed sequence on Bermuda. *P. c. cupula* in Harrington-Pembroke unindurated zone correlating with that of locality 39. *P. b. zonatus* in poorly-developed St. George's soil and in massive overlying Southampton eolianites.

43. South shore on northeast end of peninsula west of Sue Wood Bay. *P. c. cupula* in unindurated zone correlating with that of localities 39 and 41.

44. South shore on promontory west of Rocky Bay. Type locality of *P. b. sieglindae,* found in Harrington unindurated zone and overlying Pembroke eolianite.

45. Harrington Sound Road just west of Sharks Hole. Unindurated zone at road level, *P. nelsoni callosus* fairly common. Sayles's type Harrington, but may be a Pembroke unindurated zone.

46. South Road just east of Pink Beach. Type locality of *P. c. triangularis.* A well-developed Harrington-Pembroke unindurated zone exposed in a road cut, north side of road.

47. South shore at Cox's Bay. St. George's erosional surface reaches Belmont marine limestone just east of locality. St. George's rises westward over a Pembroke dune containing *P. b. zonatus.*

48. Ferry Road, halfway between Biostation and Whalebone Bay. *P. c. cupuloides* in thin exposure (less than 1 foot) of Shore Hills soil.

49. South shore just west of Hungry Bay. Well-developed brownish Harrington unindurated zone overlies Devonshire intertidal conglomerate. Devonshire fills wave-cut notch on western end of Hungry Bay.

51. South shore at Grape Bay. Second most complete superposed sequence on the island. Shore Hills soil present in solution pipes and as veneer on Belmont conglomerate. Thick intertidal Devonshire conglomerate follows, overlain by Devonshire sands and brown Harrington unindurated zone with *P. b. zonatus.* Leeward beds of a Pembroke dune follow, capped by the St. George's erosional surface.

53. Cave north of Tom Moore's Tavern. Well-developed Shore Hills soil profile within cave; type locality of *P. b. fasolti.*

55. Charles Island. Well-developed unindurated zone surrounds entire island. Richest locality on Bermuda for *P. b. zonatus.* Harrington or Pembroke, since red soil overlies unindurated zone at east end of island.

56. North shore north of intersection of North Shore Road and Coney Island Road. Shore Hills soil exposed on top of eroding cliff.

62. South shore at Simmons Beach. Massive accumulation of Southhampton eolianites, with unindurated zones separating

dunes. Three superposed layers containing *P. b. zonatus*.

63. North shore south of Gibbet Island. *P. cupula cupula* in Pembroke unindurated zone at top of cliff. *P. s. arenicolus* in unindurated zone below, at sea level.

64. South Shore Road at McGall's Hill. *P. n. nelsoni* in Harrington soil exposed at road level on south side of road.

65. North shore of Ireland Island. Shore Hills soil with *P. nelsoni nelsoni* filling Walsingham fissure.

66. Quarry on southern Ireland Island. Moderately developed St. George's soil with *P. b. zonatus*.

67. Middle Road south of Wilson's Island. *P. b. zonatus* in well-developed unindurated zone of unknown age.

68. North shore north of Coney Island Road just west of Coney Island. *P. nelsoni nelsoni* in veneer of St. George's soil superposed above section containing Belmont eolianites. Shore Hills soil and Pembroke eolianites.

69. Somerset Road at Fort Scaur. (?) Hybrid *P. bermudensis* and *P. cupula* in brown soil of unknown age exposed in road cut on east side of road.

71. Surf Bay. Patchy unindurated zone separating two eolianites. Red soil (probably Shore Hills) 4 feet above. Belmont eolianite (?).

73. Sand Quarries west of Middle Road. *P. b. zonatus* in massive deposits of poorly-consolidated upper Southampton eolianites.

75. South Shore Road just east of Horseshoe Bay. *P. b. zonatus* in massive deposits of poorly-consolidated upper Southampton eolianite exposed at south side of road. Similar deposits with abundant land snails throughout this region.

76. Intersection of Knapton Hill Road and South Road. *P. c. cupula* in unindurated pocket.

77. Knapton Hill Road at crest of Knapton Hill. *P. c. cupula* in poorly-developed unindurated zone exposed in road cut.

78. Grounds of Bermuda Biostation. Living *P. b. bermudensis* in garden of "Big Wind" cottage.

79. Government Hill Road south of ruined church. *P. b. bermudensis* living on weathered eolianite in gardens along west side of road.

80. Intersection of St. David's Road and Chapel-of-Ease lane. Empty shells of *P. b. bermudensis* found amidst decaying vegetation.

81. North Shore Road south of Crawl Point. *P. b. bermudensis* living on weathered eolianite in garden on south side of road.

82. Perfume Factory. *P. b. bermudensis* living on red soil of Perfume Factory gardens.

83. Somerset Road just south of the town of Somerset. Empty shells of *P. b. bermudensis* in gardens at roadside.

84. Lighthouse Hill Road, St. David's Island. *P. nelsoni callosus* and *P. cupula multispira* (type locality) in poorly-consolidated eolianite of uncertain age (probably Harrington-Pembroke).

85. Harrington Sound Road just east of intersection with Devil's Hole Hill Road. *P. c. triangularis* in poorly-consolidated eolianite exposed in a road cut, north side of road.

86. Paynter's Road at border of Hamilton Parish and Tucker's Town. *P. nelsoni callosus* in unindurated zone. Probably Harrington or Pembroke in age.

87. Higgs Island, Town Cut. Well-developed Harrington unindurated zone lies on patchy Devonshire conglomerate and typical Belmont marine limestone. Pembroke eolianite above. *P. b. zonatus* in continuous sequence throughout Harrington-Pembroke interval.

88. Quarry on south face of Fox's Hill, St. David's Island. *P. nelsoni callosus* and *P. c. multispira* in poorly-consolidated eolianite.

89. Prospero's Cave. Well-developed

Shore Hills Soil profile within caves; *P. nelsoni nelsoni* abundant.

91. St. David's Road south of Emily's Bay. *P. c. multispira* in poorly-consolidated eolianite exposed in road cut.

95. North Shore Road west of Bailey's Bay. *P. n. callosus* in Harrington unindurated zone and in overlying Pembroke eolianite exposed on north side of road.

97. Cambridge Beaches. *P. n. nelsoni* in extensive exposure of Shore Hills soil exposed near sea level along the western shore of Somerset Island.

100. Island west of Trunk Island in Harrington Sound. *P. s. arenicolus* in lower unindurated zone (Harrington) encircling island.

P1. "Quarry near Waterloo House, Castle Harbour. A. Gulick 1903 No. 816." *P. b. zonatus* from Shore Hills soil.

P2. "Large quarry 1/2 way between Tucker's Town and Walsingham. A. Gulick 1903!" Shore Hills soil. Type locality of *P. c. cupula* and two rejected synonyms of *P. n. nelsoni* (*P. n. discoides* and *P. n. conoides*).

P3. "Whitby, Bailey's Bay. From a cleft 2 ft. wide, 90 feet above sea level, associated with bird bones, etc. Arthur Haycock 1922!" *P. c. cupula* and *P. n. nelsoni* in Shore Hills soil.

P4. "'cupuloides' (part of original lot). 80 yards north of Harrington House, Harrington Sound. Base of 10 foot hard limestone road cutting. Arthur Haycock 1922!" Type locality of *P. c. cupuloides.*

P5. "Cave near Harrington House. H. C. Hoyt 1927!" *P. b. zonatus* in Shore Hills soil.

P6. "Castle Harbor near Harrington House." *P. b. zonatus* in Shore Hills soil.

P7. "Devonshire Marsh, Gulick's locality 818." *P. b. zonatus* from unindurated zone or eolianite. Both eastern and western color forms present with intermediates.

P8. "Benjamin Trott's sand pit, Tuckerstown, A. Gulick, 1903." Probably Harrington-Pembroke in age.

P9. "Admiral's Cave, Bermuda. Hiram Hoyt." *P. n. nelsoni* in deep red soil, almost surely Shore Hills in age.

Synopsis of localities, according to parish:

A) *St. George's Parish:* 1, 11, 12, 15, 16, 17, 18, 21, 24, 27, 48, 78, 79, 80, 84, 87, 88, 91;
B) *Hamilton Parish:* 3, 5, 9, 30, 34, 45, 53, 56, 68, 81, 82, 86, 89, 95, 100, P1, P2, P3, P4, P5, P6, P9;
C) *Tucker's Town:* 55, 71, P8;
D) *Smiths Parish:* 4, 31, 32, 35, 36, 37, 39, 40, 41, 46, 63, 64, 76, 77, 85;
E) *Devonshire Parish:* 2, 43, 44, 47, P7;
F) *Paget Parish:* 49, 51;
G) *Pembroke Parish:* 6;
H) *Warwick Parish:* 62;
I) *Southampton Parish:* 67, 73, 75;
J) *Sandys Parish:* 10, 65, 66, 69, 83, 97.

Synopsis of localities according to subspecies:

A) *P. nelsoni nelsoni*
  1. Shore Hills: 5, 9 (?), 30, 34, 65, 89, 97, P2, P3, P9
  2. Harrington-Pembroke: 64
  3. St. George's: 18, 68
B) *P. nelsoni callosus*
  1. Harrington-Pembroke: 30, 45, 84, 86, 95, P8
C) *P. superior superior*
  1. Shore Hills: 5, 9(?), 34
D) *P. superior arenicolus*
  1. Shore Hills: 11
  2. Harrington-Pembroke: 11, 63, 100, loc. ? (Bda. Museum)
E) *P. bermudensis zonatus*
  1. Shore Hills: 5, P1, P5, P6
  2. Harrington: 1, 2, 28, 49, 51, 55, 87
  3. Pembroke: 1, 6, 47, 87
  4. St. George's: 17, 31, 37, 41, 66
  5. Southampton: 17, 36, 40, 62, 73, 75
F) *P. bermudensis fasolti*
  1. Shore Hills: 53
G) *P. bermudensis siegmundi*
  1. Harrington: 10

H) *P. bermudensis sieglindae*
  1. Harrington: 44
  2. Pembroke: 44

I) *P. bermudensis bermudensis*
  1. St. George's: 11, 12, 16
  2. Southampton: 11, 15, 21, 24, 27
  3. Recent: 78, 79, 80, 81, 82, 83

J) *P. cupula cupula*
  1. Shore Hills: P2, P3
  2. Harrington-Pembroke: 32, 35, 39, 41, 43, 63, 76, 77

K) *P. cupula dalli*
  1. Harrington-Pembroke: 4

L) *P. cupula cupuloides*
  1. Walsingham: 9, P4
  2. (?) Belmont eolianite: 30, 71
  3. Shore Hills: 48, 56

M) *P. cupula multispira*
  1. (?) Harrington-Pembroke: 84, 88, 91

N) *P. cupula triangularis*
  1. Harrington-Pembroke: 46, 85

O) Hybrid *P. bermudensis-P. cupula*
  1. Shore Hills: 3
  2. Harrington: 3
  3. (?): 69

MATRIX OF MEANS FOR *P. CUPULA* (STANDARDIZED AT 5⅜ WHORLS)

	ONSEUP	LOWCOL	COLOR4	COLOR5	PRDEGR	PRWIDT	PRHIGH	WIDTH1	HEIGH1	WIDTH2	HEIGH2	WIDTH3	HEIGH3	WIDTH4	HEIGH4	WIDTH5	HEIGH5	TSIZE5
P.c. cupula																		
HP35	3.812	.173	.460	.476	557.7	1.98	.355	1.93	.588	2.90	1.00	4.17	1.74	5.86	2.99	7.81	5.42	13.23
HP37	4.089	.183	.349	.425	573.5	2.04	.338	2.01	.594	3.02	0.993	4.35	1.68	6.13	2.95	8.23	5.21	13.44
HP39	4.550	.166	.355	.414	561.1	2.01	.363	1.98	.596	2.98	0.988	4.29	1.67	5.98	2.88	7.77	5.09	12.87
HP41c	4.375	.172	.341	.374	569.8	2.03	.342	2.00	.606	3.01	1.05	4.32	1.78	5.95	3.15	7.91	5.60	13.51
HP41b	4.528	.196	.357	.389	570.5	2.02	.343	1.96	.583	2.94	1.00	4.23	1.73	5.85	3.04	7.93	5.34	13.27
HP41a	4.450	.193	.323	.369	577.6	1.99	.336	1.95	.581	2.98	0.997	4.34	1.72	6.17	3.04	8.34	5.53	13.86
HP43	4.225	.188	.293	.381	562.4	2.00	.322	1.99	.567	3.01	1.00	4.42	1.74	6.28	3.17	7.80	5.82	13.82
P63		.187	.408	.436	551.1	1.98	.301	1.89	.574	2.86	1.02	4.06	1.87	5.42	3.45	6.75	5.92	12.66
SHP3	3.625	.099	.365	.410	607.9	2.09	.356	2.00	.637	2.98	1.16	4.16	2.13	5.49	3.80	6.97	6.43	13.40
SHP2	4.042	.200	.375	.459	615.7	2.25	.383	2.15	.716	3.15	1.33	4.26	2.43	5.46	4.32	6.86	7.10	13.96
P.c. triangularis																		
HP46		.195	.369		544.8	1.78	.315	1.72	.545	2.63	0.910	3.83	1.55	5.48	2.69	7.43	4.62	12.05
HP85		.219	.145	.129	558.9	1.83	.319	1.81	.558	2.74	0.979	3.99	1.68	5.75	2.91	8.00	5.17	13.17
P.c. cupuloides																		
W9		.170			585.6	1.91	.385	1.80	.679	2.67	1.14	3.77	1.90	5.13	3.22	6.47	5.57	12.05
WP4		.177			549.5	1.83	.389	1.78	.672	2.68	1.13	3.76	1.92	5.12	3.31	6.45	5.56	12.02
SH56		.194			597.4	1.79	.365	1.64	.603	2.48	1.00	3.55	1.66	4.90	2.83	6.31	4.84	11.15
B30		.275	.456	.427	580.7	1.85	.409	1.74	.700	2.59	1.18	3.64	1.99	4.97	3.43	6.20	5.82	12.02
SH18		.256	.491	.440	601.6	1.91	.348	1.82	.555	2.68	0.908	3.76	1.54	5.16	2.62	6.72	4.52	11.25
B71					560.7	1.78	.327	1.69	.571	2.56	0.981	3.69	1.65	5.12	2.86	6.73	5.19	11.91
P.c. multispira																		
HP84 and 88		.193			558.3	1.62	.351	1.51	.574	2.25	0.974	3.13	1.66	4.15	2.76	5.30	4.47	9.76
P.c. dalli																		
HP4		.191			518.3	1.52	.325	1.44	.632	2.11	1.21	2.81	2.19	3.42	3.74	3.92	5.78	9.70

Matrix of means for *P. cupula* (continued)

	RATIO5	PSANGL	DANGLE	KVALUE	INFORM	UMBILC	APWIDT	ALDIVW	APHIGH	RELSPI	INNLIP	OUTCAR	LOWOFF	LOWECC	UPPOFF	UPPECC	TOTECC	Total height	Total width
P.c. cupula																			
HP35	1.44	45.9	55.8	2.07	.222	1.87	8.42	1.34	6.26	.632	6.14	3.81	3.39	.403	2.94	.349	.248	9.9	17.7
HP37	1.58	43.0	55.9	2.07	.201	2.02	8.57	1.30	6.60	.667	6.33	3.87	3.86	.451	2.92	.341	.208	9.9	18.4
HP39	1.53	42.3	56.5	2.23	.184	2.08	8.25	1.28	6.43	.691	5.94	3.57	3.26	.396	2.67	.323	.281	9.3	17.5
HP41c	1.41	45.7	58.3	2.06	.239	2.08	8.32	1.37	6.07	.626	5.83	3.86	3.73	.449	3.08	.370	.181	9.7	17.7
HP41b	1.49	42.5	56.5	2.09	.216	1.89	8.12	1.31	6.18	.651	5.78	3.84	3.47	.427	2.96	.365	.208	9.5	17.7
HP41a	1.51	44.0	54.4	2.06	.218	2.03	8.73	1.31	6.66	.666	6.12	4.18	3.93	.450	3.28	.376	.174	10.0	18.4
HP43	1.37	46.2	55.2	2.10	.229	1.89	8.07	1.30	6.23	.636	5.89	3.94	3.62	.448	3.10	.384	.167	9.8	17.5
P63	1.19	57.6	58.6	2.42	.251	1.42	6.91	1.23	5.60	.571	5.54	3.32	3.43	.496	2.06	.299	.205	9.8	14.7
SHP3	1.09	55.0	60.3	2.38	.276	1.57	7.14	1.22	5.86	.548	5.71	3.63	3.41	.477	2.32	.326	.197	10.7	15.6
SHP2	0.97	56.9	63.3	2.58	.303	1.20	7.24	1.10	6.55	.546	5.69	3.80	3.68	.509	2.40	.332	.159	12.0	16.2
P.c. triangularis																			
HP46	1.61	42.4	59.1	1.94	.220	2.13	7.80	1.25	6.23	.670	5.64	3.64	3.26	.418	2.68	.344	.238	9.3	17.0
HP85	1.55	43.1	56.3	1.85	.247	1.77	8.80	1.30	6.76	.669	6.02	4.40	4.00	.455	3.50	.398	.147	10.1	18.1
P.c. cupuloides																			
W9	1.16	54.8	58.2	2.15	.282	1.34	6.92	1.18	5.86	.586	5.44	3.28	3.22	.465	2.08	.300	.235	10.0	14.9
WP4	1.16	53.8	58.2	2.19	.278	1.47	6.54	1.16	5.63	.580	5.34	3.25	2.92	.447	2.05	.313	.240	9.7	14.7
SH56	1.30	51.7	56.2	2.08	.254	1.54	6.65	1.22	5.46	.620	5.16	3.06	2.78	.417	2.07	.311	.271	8.8	14.4
B30	1.07	58.8	59.6	2.22	.296	1.45	6.57	1.17	5.64	.576	5.06	3.30	3.42	.520	2.17	.330	.149	9.8	14.2
SH18	1.48	45.2	59.4	2.19	.208	1.96	6.87	1.24	5.56	.654	5.41	3.06	2.30	.335	2.11	.308	.357	8.5	15.0
B71	1.30	53.3	60.0	2.08	.255	1.31	7.34	1.19	6.15	.627	5.59	3.52	3.45	.558	2.40	.328	.206	9.8	15.0
P.c. multispira																			
HP84 and 88	1.19	49.6	58.3	2.24	.276	1.05	5.54	1.29	4.29	.613	4.42	2.34	2.18	.393	1.39	.250	.356	7.0	12.2
P.c. dalli																			
HP4	0.68	70.3	60.3	2.95	.418	0.68	4.09	0.97	4.20	.494	3.40	2.35	2.14	.524	1.35	.330	.146	8.5	8.9

Matrix of means for *P. nelsoni* and *P. superior* (standardized at 40 mm height + width)

	COLOR5	LOWCOL	PRWIDT	PRHIGH	WIDTH2	HEIGH2	WIDTH3	HEIGH3	WIDTH4	HEIGH4	WIDTH5	HEIGH5	TSIZE5	RATIO5	DANGLE
P.n. nelsoni															
SH5 (Main)		.323	2.19	.318	3.39	1.21	4.85	2.28	6.76	4.03	9.46	6.79	16.25	1.39	56.1
SH5 (Bird)		.328	2.44	.318	3.75	1.22	5.19	2.47	6.87	4.60	9.17	7.72	16.89	1.19	57.3
SH5 (Coquina)	.092	.235	2.25	.281	3.38	1.01	4.81	1.98	6.58	3.71	8.94	6.23	15.18	1.43	56.0
SH89		.395	2.37	.356	3.59	1.40	5.07	2.51	7.13	4.54	10.07	7.56	17.78	1.31	57.7
SHP9		.336	2.20	.287	3.39	1.22	4.87	2.31	6.80	4.15	9.39	7.10	16.49	1.32	58.0
SHP2		.304	2.43	.211	3.78	0.863	5.46	1.95	7.71	3.76	11.17	6.41	17.59	1.74	58.2
SHP3	.359	.324	2.34	.272	3.53	0.967	5.03	1.94	6.96	3.57	9.75	6.25	16.00	1.60	54.0
SH30		.387	2.38	.283	3.63	1.24	5.19	2.37	7.28	4.32	10.13	7.31	17.44	1.39	56.9
SH65	.498	.355	2.40	.290	3.66	1.12	5.28	2.17	7.50	4.03	10.94	7.17	18.11	1.52	55.3
SH97		.294	2.05	.272	3.35	0.848	5.10	1.68	7.34	3.47	10.71	6.62	17.34	1.62	58.5
HP64		.444	2.28												
SG18	.400	.341	2.35	.238	3.71	0.997	5.36	2.08	7.68	3.85	11.00	6.83	17.83	1.61	55.3
SG68	.330	.330	2.41	.314	3.75	1.21	5.34	2.35	7.56	4.24	10.70	7.19	17.89	1.49	56.4
P.n. callosus															
HP95		.288	2.04	.365	3.17	1.16	4.61	2.10	6.67	3.68	9.61	6.40	16.01	1.50	55.0
HP30		.287	1.95	.342	2.92	1.04	4.21	1.92	6.01	3.59	8.38	6.20	14.58	1.35	56.8
HP45	.391	.214	1.83	.323	2.83	1.01	4.09	1.89	5.71	3.39	7.78	5.89	13.67	1.32	57.2
HP86		.224	1.85	.310	2.95	0.937	4.36	1.79	6.28	3.21	8.94	5.71	14.66	1.57	56.7
HPP8	.631	.290	2.00	.391	3.04	1.26	4.39	2.19	6.15	3.76	8.69	6.29	14.98	1.38	56.5
HP(?)[1]		.237	1.84	.312	2.75	1.06	3.97	1.93	4.87	3.41	7.47	5.94	13.41	1.26	58.0
HP84 and 88			2.04	.307	2.99	1.03	4.20	1.82	5.82	3.07	8.24	5.03	13.27	1.64	53.7
P.s. superior															
SH34	.277	.250	2.40	.305	3.50	1.21	4.76	2.48	6.12	4.61	7.37	7.41	14.76	0.994	59.6
SH5 (Bird)	.272	.277	2.13	.335	3.17	1.25	4.29	2.37	5.39	4.26	6.67	7.01	13.67	0.951	61.2
SH9[2]		.227	2.54	.372	3.65	1.56	4.84	3.12	6.18	5.58	7.44	9.37	16.81	0.794	54
P.s. arenicolus															
HP63		.206	1.95	.330	2.96	1.06	4.23	1.93	5.82	3.50	7.60	6.18	13.78	1.23	56.6
HP100		.221	1.97	.333	3.04	1.03	4.36	1.86	6.12	3.45	8.18	6.26	14.45	1.31	56.8
HP11		.221	2.05	.314	3.20	1.07	4.48	2.07	6.07	3.82	7.75	6.67	14.42	1.16	57.3
HP(?)[3]		.201	2.05	.348	3.07	1.21	4.29	2.28	5.67	4.15	7.17	7.10	14.27	1.01	55.8

[1] From Sayles collection labelled "S. Shore Harrington Sound."

[2] Either *P.s. superior* or *P.n. nelsoni.*

[3] From Bermuda Museum labelled "Bermuda."

MATRIX OF MEANS FOR *P. NELSONI* AND *P. SUPERIOR* (continued)

	KVALUE	INFORM	UMBILC	APLONG	ALDIVW	APHIGH	RELSPI	INNLIP	OUTCAR	LOWOFF	LOWECC	UPPOFF	UPPECC	Total height	CALLUS
P.n. nelsoni															
SH5 (Main)	1.86	260	2.26	11.75	1.21	9.69	.629	8.76	5.82	2.32	.197	4.02	.342	15.4	0.229
SH5 (Bird)	2.28	240	2.60	11.84	1.28	9.27	.606	8.18	6.07	5.21	.440	4.42	.373	15.3	0.033
SH5 (Coquina)	2.14	217	2.23	11.73	1.23	9.52	.610	8.39	5.86	4.87	.415	4.42	.377	15.6	0.056
SH89	1.89	270	2.54	12.11	1.26	9.63	.651	8.44	6.20	3.76	.310	4.26	.351	14.8	0.102
SHP9	1.87	275	2.38	12.44	1.32	9.45	.622	8.59	6.03	2.98	.239	4.34	.349	15.2	0.020
SHP2	2.07	173	3.05	13.29	1.43	9.31	.700	8.88	6.28	3.76	.283	5.03	.378	13.3	0.010
SHP3	2.01	197													0.593
SH30	1.80	262	2.81	12.17	1.27	9.58	.665	8.32	6.23	4.12	.339	4.23	.347	14.4	0.108
SH65	1.96	224	2.68	12.65	1.37	9.26	.652	8.82	5.95	2.68	.212	4.32	.341	14.2	0.072
SH97	2.16	171	2.84	12.71	1.35	9.39	.676	9.12	6.50	2.93	.230	4.67	.368	13.9	0.000
HP64															
SG18	1.88	221	2.98	12.62	1.42	8.88	.648	8.33	6.55	3.57	.283	4.84	.383	13.7	0.190
SG68	1.85	242	2.56	12.54	1.35	9.27	.648	8.32	6.13	3.72	.297	4.61	.368	14.3	0.079
P.n. callosus															
HP95	1.81	254	2.07	11.77	1.21	9.73	.653	8.53	5.76	2.83	.240	3.75	.319	14.9	0.977
HP30	1.97	240	2.04	11.59	1.16	9.97	.619	8.53	6.06	2.74	.236	3.88	.335	16.1	0.557
HP45	2.03	246	1.47	11.38	1.13	10.04	.608	8.62	6.00	3.82	.336	3.87	.340	16.5	0.688
HP86	1.92	215	2.08	12.08	1.25	9.63	.629	8.94	6.35	4.98	.413	4.33	.358	15.3	1.157
HPP8	1.77	290	1.89	11.19	1.19	9.40	.610	8.42	5.61	3.59	.320	3.60	.321	15.4	0.659
HP(?)[1]	2.00	270	1.35	11.26	1.17	9.66	.589	8.41	5.95	4.48	.398	3.72	.330	16.4	0.419
HP84 and 88	1.80	246	2.43	10.91	1.15	9.52	.591	8.48	5.88	3.48	.319	3.79	.348	16.1	1.940
P.s. superior															
SH34	2.82	258	1.41	11.01	1.09	10.10	.552	7.59	6.25	4.67	.424	4.23	.384	18.3	0.000
SH5 (Bird)	2.66	290	1.16	10.43	1.04	10.03	.528	7.37	6.34	5.59	.536	4.45	.427	19.0	0.033
SH9[2]	2.60	327													
P.s. arenicolus															
HP63	2.23	243	1.53	10.71	1.15	9.31	.538	8.11	5.77	5.09	.475	3.73	.349	17.3	0.082
HP100	2.18	227	1.96	11.12	1.10	10.13	.603	8.63	5.83	4.94	.444	3.57	.321	16.8	0.144
HP11	2.37	238	1.56	10.74	1.11	9.67	.559	8.14	5.79	4.48	.417	3.21	.299	17.3	0.098
HP(?)[3]	2.40	280	1.65	10.52	1.08	9.29	.510	7.62	5.91	5.65	.537	3.87	.368	18.2	0.016

[1] From Sayles collection labelled "S. Shore Harrington Sound."

[2] Either *P.s. superior* or *P.n. nelsoni.*

[3] From Bermuda Museum labelled "Bermuda."

MATRIX OF MEANS FOR *P. BERMUDENSIS* (STANDARDIZED AT 30 MM HEIGHT + WIDTH)

	ONSEUP	ONSELO	LOWCOL	COLOR3	COLOR4	COLOR5	PRDEGR	PRWIDT	PRHIGH	WIDTH1	HEIGH1	WIDTH2	HEIGH2	WIDTH3	HEIGH3	WIDTH4	HEIGH4	WIDTH5	HEIGH5
P.b. zonatus																			
SH5	5.12	3.58	.322		.708	.741	607.7	2.16	.289	2.12	.487	3.20	0.843	4.59	1.50	6.38	2.88	8.52	5.46
SHP5			.364				653.6	2.20	.309	2.09	.509	3.12	0.879	4.48	1.57	6.02	2.97	7.76	5.43
SHP6	5.47	4.59	2.95		.605	.682	612.1	2.14	.288	2.08	.487	3.07	0.843	4.37	1.48	5.97	2.71	7.80	5.05
SHP1	5.31	4.14	.306		.610	.650	598.3	2.19	.316	2.11	.494	3.20	0.814	4.58	1.46	6.30	2.84	8.46	5.20
H1	5.17	4.35	.393		.800	.822	651.9	2.14	.327	2.17	.588	3.25	1.08	4.68	1.96	6.49	3.65	8.58	6.72
H87	5.12	4.13	.336		.774	.779	712.1	2.24	.362	2.25	.639	3.36	1.18	4.80	2.08	6.57	3.73	8.62	6.68
H2	5.18	4.32	3.67		.769	.791	633.7	2.18	.344	2.21	.596	3.36	1.10	4.85	2.01	6.82	3.71	9.04	6.79
H49		5.08	.415		.503	.506	617.2	2.17	.336	2.21	.618	3.33	1.11	4.85	1.95	6.73	3.63	8.81	6.65
H51		4.32	.405		.478	.467	624.6	2.14	.345	2.20	.632	3.32	1.13	4.84	2.01	6.68	3.73	8.59	6.78
P6		3.23	.375	.482	.518	.568	660.2	2.17	.363	2.21	.661	3.35	1.24	4.90	2.16	6.80	4.00	8.80	7.15
P1			.370		.809	.836	583.7	2.14	.327	2.16	.610	3.31	1.16	4.88	2.07	6.87	4.00	9.28	7.14
P87			.368		.869	.877	620.7	2.17	.334	2.22	.625	3.36	1.16	4.88	2.11	6.75	3.95	8.78	7.13
P50		4.09	.356	.490	.476	.477	657.2	2.20	.347	2.22	.639	3.36	1.13	4.90	2.03	6.82	3.83	8.86	6.85
SG17			.383				595.2	2.09	.320	2.07	.567	3.15	1.02	4.52	1.80	6.35	3.31	8.49	6.07
SG37	5.00	4.04	.410		.786	.788	618.5	2.17	.324	2.11	.581	3.18	1.05	4.58	1.85	6.28	3.52	8.19	6.41
SG41	5.10	3.88	.374		.746	.779	619.0	2.14	.336	2.12	.581	3.19	1.09	4.56	1.87	6.41	3.39	8.55	6.12
SG31			.394		.753	.783	611.7	2.17	.285	2.18	.567	3.36	1.09	4.92	2.05	6.76	4.00	9.15	7.19
SG66			.309				597.1	1.99	.291	2.02	.538	3.08	0.981	4.49	1.83	6.21	3.45	8.16	6.31
S17			.390			.769	636.5	2.12	.372	2.17	.654	3.28	1.16	4.78	2.06	6.65	3.85	8.97	7.00
S36	4.80	4.05	.389		.820	.792	691.8	2.17	.349	2.27	.618	3.44	1.16	5.01	2.11	6.93	4.07	9.29	7.34
S75		4.29	.430		.696	.663	709.0	2.20	.344	2.25	.639	3.41	1.16	4.98	2.06	6.74	4.01	8.60	7.14
S73		4.39	.361		.521	.492	697.6	2.14	.403	2.17	.719	3.31	1.26	4.87	2.23	6.62	4.26	8.94	7.83
P.b. fasolti																			
SH53		5.41	.293				548.1	2.00	.247	1.98	.421	3.03	0.734	4.43	1.26	6.26	2.35	8.77	4.25
P.b. siegmundi																			
H10		4.53	.328		.441	.428	659.2	2.13	.385	2.19	.683	3.36	1.23	4.95	2.14	7.12	3.89	9.53	7.04
P.b. sieglindae																			
H44	5.38	4.50	.379		.752	.769	629.6	2.18	.338	2.20	.574	3.36	1.03	4.92	1.87	7.09	3.39	9.87	6.11
P44		4.82	.374			.658	621.1	2.17	.345	2.22	.581	3.40	1.03	5.03	1.90	7.30	3.49	9.95	6.59
P.b. bermudensis																			
SG16			.300				593.4	2.11	.350	2.09	.639	3.20	1.15	4.69	2.01	6.79	3.52	9.74	6.73
S27			.310				664.2	2.16	.424	2.23	.718	3.41	1.32	5.09	2.26	7.27	4.16	9.62	6.97
S21b			.313			.734	629.7	2.16	.343	2.18	.618	3.34	1.10	4.94	1.95	7.32	3.46	10.27	6.28
S21a			.289			.644	600.1	2.12	.362	2.17	.661	3.32	1.17	4.91	2.04	7.24	3.72	9.76	6.42
R80			.350				620.8	2.05	.351	2.01	.668	3.08	1.23	4.44	2.24	6.19	4.03	8.08	6.55
R79			.349				593.0	2.08	.381	2.09	.705	3.18	1.29	4.69	2.25	6.73	4.04	9.07	7.03
R78			.315				584.7	2.04	.409	2.04	.719	3.07	1.31	4.48	2.32	6.31	4.16	8.09	6.92
R82			.285				584.2	2.06	.360	2.07	.661	3.12	1.21	4.51	2.20	6.34	3.92	8.21	6.67
R81			.313				634.4	2.11	.401	2.14	.719	3.23	1.31	4.69	2.24	6.73	3.96	9.00	6.68
R83			.335				571.5	2.04	.389	2.05	.712	3.10	1.29	4.53	2.27	6.44	4.12	8.61	6.88
hybrids *P. cupula* × *P. bermudensis*																			
269		2.86	.236	.275	.270	.261	635.3	2.20	.438	2.16	.821	3.26	1.50	4.71	2.72	6.04	5.09	7.66	8.64
H3			.261				552.5	2.04	.332					4.40	1.84	5.98	3.39	7.72	6.10

MATRIX OF MEANS FOR *P. BERMUDENSIS* (continued)

	TSIZE5	RATIO5	PSANGL	DANGLE	KVALUE	INFORM	UMBILC	APLONG	ALDIVW	APHIGH	RELSPI	INNLIP	OUTCAR	LOWOFF	LOWECC	UPPOFF	UPPECC	Total height	CALLUS
P.b. zonatus																			
SH5	13.98	1.56	43.8	56.0	2.32	.173	2.38	8.79	1.19	7.37	.676	6.63	4.12	2.79	.317	2.86	.326	10.9	.223
SHP5	13.19	1.42	51.5	59.6	2.42	.184	2.22	8.86	1.21	7.34	.667	6.68	4.08	3.26	.368	2.76	.311	11.0	.180
SHP6	12.85	1.55	44.8	59.7	2.29	.186	2.40	8.54	1.17	7.29	.657	6.53	4.06	3.24	.380	2.73	.320	11.1	.141
SHP1	13.66	1.63	43.6	58.4	2.37	.158	2.26	8.97	1.23	7.27	.667	6.88	4.06	3.24	.361	2.90	.323	10.9	.151
H1	15.30	1.28	50.5	58.5	2.22	.241	2.01	8.80	1.26	6.96	.621	6.44	4.33	4.01	.456	3.09	.351	11.2	.259
H87	15.30	1.29	50.1	58.4	2.18	.244	1.92	8.75	1.30	6.75	.619	6.39	4.25	4.08	.466	3.02	.346	10.9	.269
H2	15.83	1.33	45.9	54.7	2.16	.227	1.74	8.84	1.35	6.55	.618	6.36	4.02	2.70	.452	2.83	.337	10.6	.341
H49	15.46	1.32	50.3	56.5	2.14	.238	1.96	8.87	1.37	6.48	.623	6.31	4.23	3.93	.443	3.27	.369	10.4	.259
H51	15.37	1.27	51.4	58.0	2.21	.231	2.07	8.71	1.32	6.59	.605	6.12	4.48	4.05	.465	3.32	.381	10.9	.265
P6	15.95	1.23	51.5	58.6	2.13	.260	1.89	8.70	1.33	6.57	.597	6.23	4.32	3.83	.440	3.01	.346	11.0	.200
P1	16.42	1.29	45.8	59.1	2.08	.250	1.69	9.02	1.31	6.91	.634	6.35	4.57	4.16	.461	3.36	.373	10.9	.295
P87	15.92	1.23	47.8	59.4	2.18	.244	1.74	8.72	1.28	6.81	.619	6.31	4.48	4.60	.528	3.15	.361	11.0	.239
P50	15.71	1.29	49.8	56.3	2.18	.234	1.91	8.81	1.30	6.76	.620	6.20	4.50	4.26	.483	3.28	.372	10.9	.193
SG17	14.56	1.40	46.4	57.8	2.13	.224	2.22	8.63	1.28	6.76	.644	6.30	4.00	3.76	.435	2.81	.326	10.5	.164
SG37	14.61	1.28	50.0	58.2	2.28	.229	2.00	8.47	1.29	6.55	.570	6.47	4.01	3.81	.449	2.69	.317	11.5	.229
SG41	14.67	1.40	44.2	54.3	2.08	.236	1.77	8.95	1.37	6.55	.618	6.57	3.91	3.81	.425	2.75	.307	10.6	.111
SG31	16.36	1.27	47.9	55.8	2.21	.241	1.70	8.56	1.29	6.63	.603	6.37	4.26	4.06	.475	3.09	.362	11.0	.177
SG66	14.47	1.29	51.6	57.0	2.24	.225	2.03	8.81	1.28	6.87	.608	6.19	4.25	3.74	.425	3.16	.359	11.3	.010
S17	15.98	1.28	50.8	57.0	2.12	.245	1.99	8.83	1.28	6.92	.635	6.32	4.29	4.03	.456	3.07	.347	10.9	.275
S36	16.63	1.27	47.5	57.2	2.22	.236	1.80	9.02	1.35	6.70	.644	6.49	4.23	4.01	.449	2.99	.331	10.4	.236
S75	15.74	1.20	52.3	57.9	2.30	.242	2.03	8.74	1.20	7.26	.660	6.68	4.30	4.26	.487	2.83	.324	11.0	.465
S73	16.77	1.14	53.0	59.5	2.21	.262	1.92	8.59	1.19	7.21	.655	6.39	4.30	4.37	.508	2.79	.325	11.0	.551
P b. fasolti																			
SH153	13.02	2.06	32.2	53.0	2.02	.160	3.01	9.35	1.25	7.48	.748	6.63	4.05	1.70	.182	3.09	.330	10.0	.000
P.b. siegmundi																			
H10	16.57	1.35	45.1	54.3	1.99	.250	2.34	9.32	1.42	6.55	.662	6.05	4.35	3.04	.326	3.49	.374	9.9	.098
P.b. sieglindae																			
H44	15.98	1.61	36.7	55.0	1.95	.207	2.03	9.35	1.41	6.65	.693	6.64	4.14	2.39	.256	3.15	.336	9.6	.102
P44	16.54	1.51	39.4	54.7	2.03	.210	1.82	9.18	1.41	6.49	.656	6.48	4.24	2.53	.276	3.07	.334	9.9	.079
P.b. bermudensis																			
SG16	16.47	1.45	38.8	53.8	1.82	.250	2.43	9.37	1.35	6.95	.695	6.57	4.40	3.16	.337	3.49	.372	10.0	.000
S27	16.59	1.38	41.7	53.9	1.91	.262	2.11	9.48	1.39	6.81	.668	6.63	4.40	4.23	.446	3.44	.363	10.2	.000
S21b	16.54	1.64	34.4	53.3	1.82	.226	2.51	9.45	1.41	6.70	.720	6.53	4.24	2.47	.261	3.34	.354	9.3	.000
S21a	16.18	1.52	38.6	55.1	1.85	.244	2.47	9.52	1.41	6.77	.691	6.73	4.45	3.98	.418	3.41	.358	9.8	.000
R80	14.62	1.23	43.2	54.3	2.03	.284	2.09	8.92	1.28	6.95	.644	6.52	4.45	3.57	.401	3.39	.380	10.8	.000
R79	16.10	1.29	45.2	56.4	1.91	.283	2.23	8.67	1.20	7.24	.652	6.49	4.03	2.86	.329	3.64	.420	11.1	.000
R78	15.02	1.17	46.7	54.9	2.01	.293	2.26	8.45	1.29	6.55	.570	6.41	3.62	3.56	.421	2.64	.313	11.5	.000
R82	14.88	1.23	45.5	56.0	2.03	.273	2.22	8.83	1.22	7.26	.648	6.57	4.16	3.41	.386	3.17	.359	11.2	.000
R81	15.69	1.35	40.7	55.3	1.86	.285	2.45	8.80	1.21	7.28	.668	6.41	4.03	2.76	.314	2.97	.338	10.9	.000
R83	15.49	1.25	41.8	56.2	1.96	.289	2.14	8.72	1.26	6.91	.628	6.45	4.15	3.36	.386	3.03	.348	11.0	.000
hybrids *P. cupula* × *P. bermudensis*																			
?69	16.30	0.89	60.8	61.8	2.44	.326	1.60	7.56	1.11	6.81	.536	5.82	4.11	4.45	.588	2.81	.372	12.7	.252
H3	13.82	1.27	53.9	55.7	2.35	.319	1.63	8.72	1.27	6.86	.602	6.56	4.20	4.00	.459	2.98	.342	11.4	.000

Plate 1. *Poecilozonites cupula* and coloration of *P. bermudensis*

Figures

1. *Poecilozonites cupula cupula* Gulick. From locality 63, Pembroke Formation. Coloration 12^{n}3. MCZ 29006. × 2½.

2. *Poecilozonites cupula dalli* (Gulick). From locality 4, Harrington Formation. Coloration 02^{n}3. MCZ 29007. × 2½.

3. *Poecilozonites cupula cupuloides* (Peile). From locality 9, Walsingham Formation. Coloration 1^{f}00. MCZ 29008. × 2½.

4. *Poecilozonites cupula multispira* new subsp. Holotype from locality 84, Harrington Formation. Coloration 023. MCZ 29009. × 2½.

5. *Poecilozonites cupula triangularis* new subsp. Holotype from locality 46, Harrington Formation. Coloration 023. MCZ 29010. × 2½.

6. *Poecilozonites bermudensis zonatus* Verrill. From locality 6, Pembroke Formation. Illustrated to show coloration of this subspecies in western Bermuda—023. MCZ 28995. × 2.

7. *Poecilozonites bermudensis zonatus* Verrill. From locality 41, Southampton Formation. Illustrated to show coloration of this subspecies in eastern Bermuda—123. MCZ 28994. × 2.

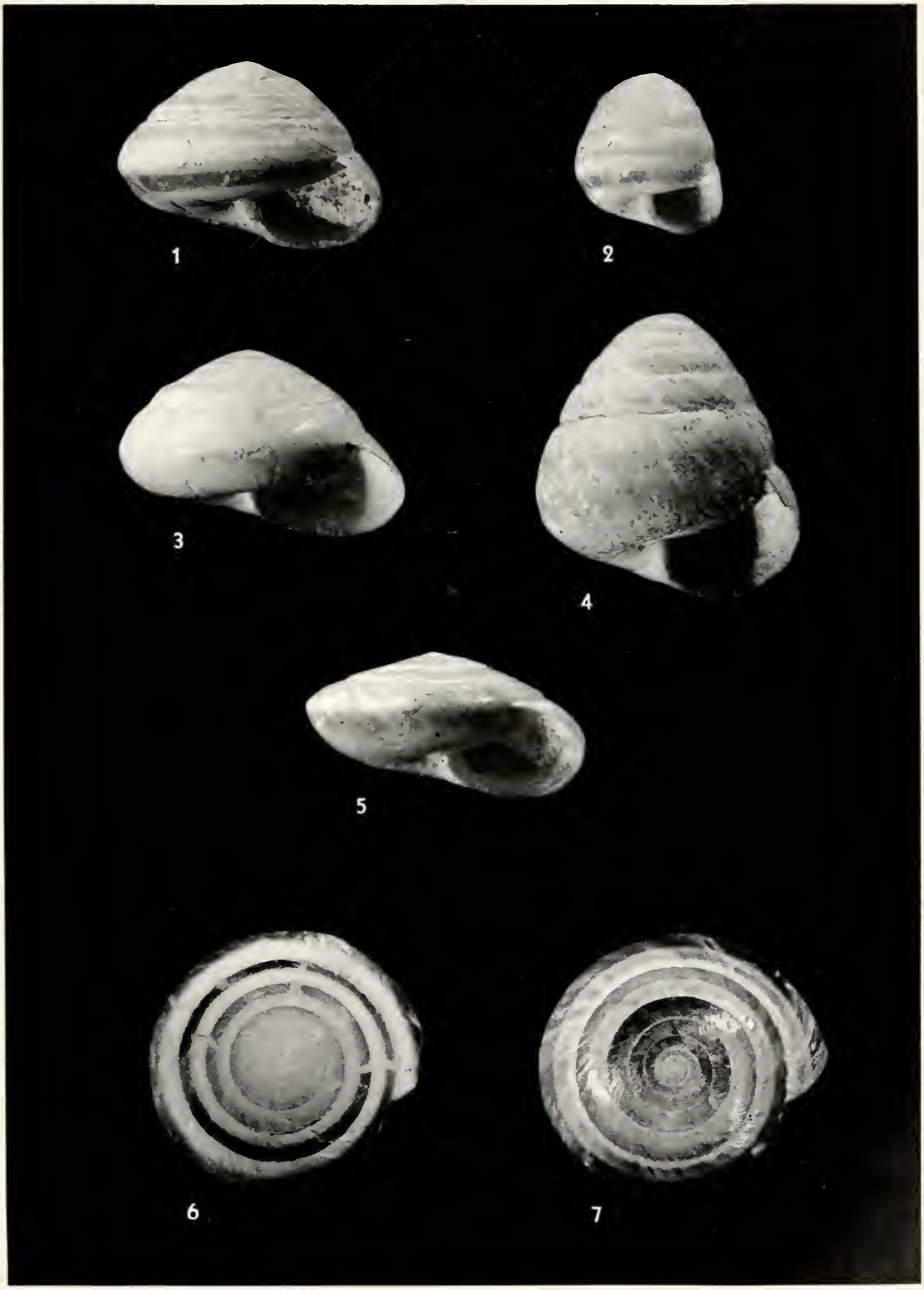


PLATE 1

Plate 2. *Poecilozonites nelsoni* and *P. superior*

Figures 1–5 are arranged to show increasing height of spire among local populations of *P.n. nelsoni.*

Figures

1. *Poecilozonites nelsoni nelsoni* (Bland). Holotype of *P. nelsoni discoides* Gulick. From locality P2, Shore Hills Formation. ANSP 58084. × 1.

2. *Poecilozonites nelsoni nelsoni* (Bland). From locality 18, St. George's Formation. MCZ 29011. × 1.

3. *Poecilozonites nelsoni nelsoni* (Bland). From locality 30, Shore Hills Formation. MCZ 29012. × 1.

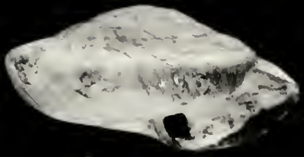
4. *Poecilozonites nelsoni nelsoni* (Bland). Topotype of *P. nelsoni conoides* Verrill. From locality P2, Shore Hills Formation. MCZ 29013. × 1.

5. *Poecilozonites nelsoni nelsoni* (Bland) or *P. superior superior* new sp. From locality 9, Shore Hills Formation. MCZ 29014. × 1.

6. *Poecilozonites nelsoni nelsoni* (Bland). Would-be holotype of Pilsbry's manuscript name *P. nelsoni gulickiana.* From locality P3, Shore Hills Formation. ANSP 131582. × 1.

7. *Poecilozonites nelsoni nelsoni* (Bland). From locality 5 (Bird Fissure), Shore Hills Formation. MCZ 29015. × 1.

8. *Poecilozonites superior superior* new sp. Holotype from locality 5 (Bird Fissure), Shore Hills Formation. MCZ 29016. × 1.



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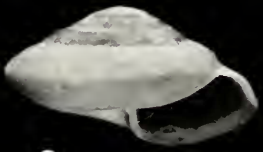

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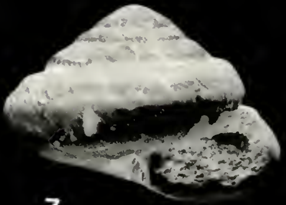

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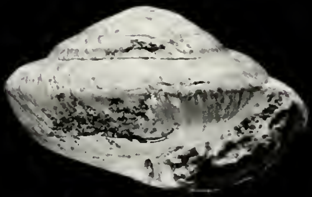

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PLATE 2

Plate 3. *Poecilozonites nelsoni, P. superior,* and protoconch of *P. bermudensis*

Figures

1. *Poecilozonites nelsoni callosus* Gulick. From locality 45, Harrington Formation. Note 023 coloration. MCZ 29017. × 1.

2. *Poecilozonites nelsoni callosus* Gulick. Holotype from locality P8, Harrington-Pembroke Formations. ANSP 58086. × 1.

3. *Poecilozonites nelsoni callosus.* From locality 84, Harrington-Pembroke Formations. MCZ 29018. × 1.

4. *Poecilozonites superior arenicolus* new subsp. Holotype from locality 11, Pembroke Formation. MCZ 29019. × 1.

5. *Poecilozonites superior arenicolus* new subsp. From Bermuda Museum, locality unknown. Note 103 coloration. MCZ 29020. × 1.

6. *Poecilozonites bermudensis bermudensis* (Pfeiffer). From locality 78. Recent. ½ whorled specimen to show form of juvenile. MCZ 29000. × 18.

7. *Poecilozonites bermudensis bermudensis* (Pfeiffer). From locality 78. Recent. Note transition from protoconch to post-embryonic shell ½ whorl before terminus. MCZ 29000. × 18.

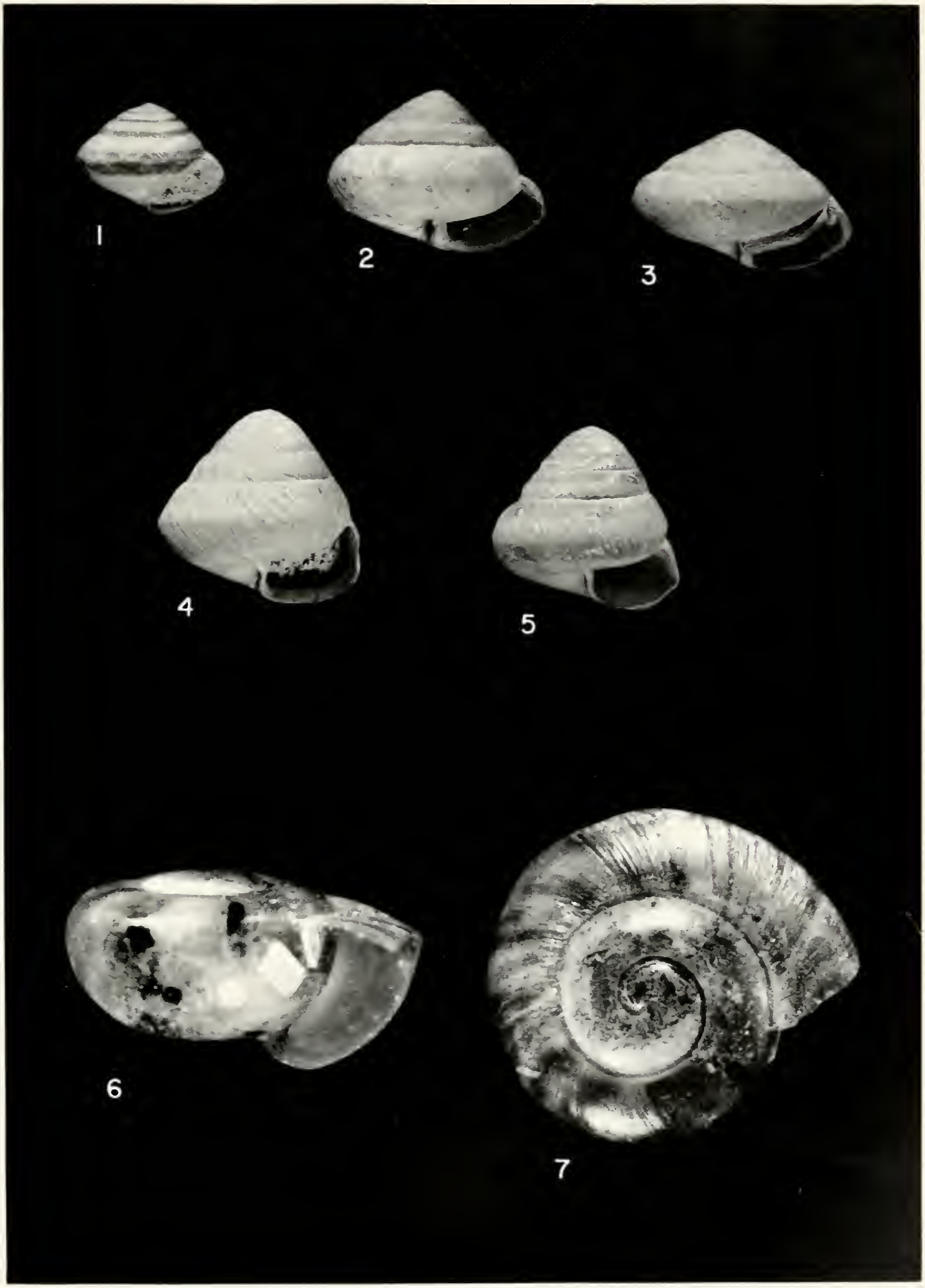


PLATE 3

Plate 4. *Poecilozonites bermudensis*

Figures 1–6 depict ancestral and paedomorphic subspecies of this taxon. Figure 1 enlarged × 2; others enlarged to same width. Actual widths of specimens: 1 = 19.7 mm, 2 = 11.5 mm, 3 = 22.2 mm, 4 = 21.5 mm, 5 = 20.2 mm, 6 = 23.0 mm.

Figures

1. *Poecilozonites bermudensis zonatus* Verrill. From locality 73, Southampton Formation. MCZ 28987.

2. *Poecilozonites bermudensis zonatus* Verrill. From locality 73, Southampton Formation. Juvenile specimen (3 6/8 whorls) enlarged to show similarity of shape with adult paedomorphs. MCZ 28988.

3. *Poecilozonites bermudensis fasolti* new subsp. Holotype from locality 53, Shore Hills Formation. MCZ 28989.

4. *Poecilozonites bermudensis siegmundi* new subsp. Holotype from locality 10, Harrington Formation. MCZ 28990.

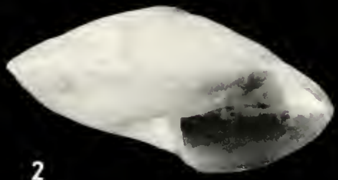
5. *Poecilozonites bermudensis sieglindae* new subsp. Holotype from locality 44, Harrington Formation. MCZ 28991.

6. *Poecilozonites bermudensis bermudensis* (Pfeiffer). From locality 21, Southampton Formation. MCZ 28992.

7. *Poecilozonites bermudensis bermudensis* (Pfeiffer). From locality 78, Recent. Illustrated to show persistence of juvenile color flammulation in paedomorphs. MCZ 28993. × 2.

8. *Poecilozonites bermudensis zonatus* Verrill. From locality 41, Southampton Formation. Typical coloration of non-paedomorphs. MCZ 28994. × 2.

1



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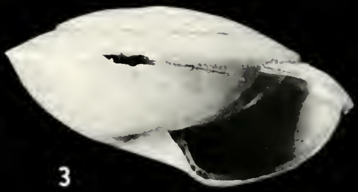

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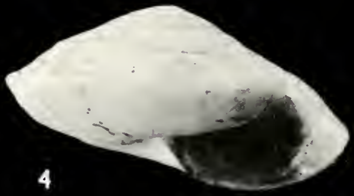

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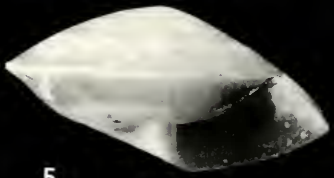

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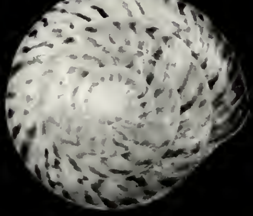

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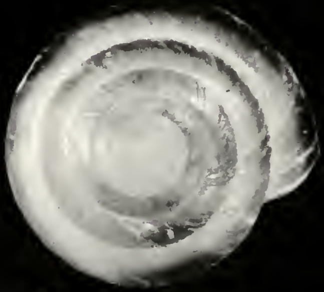

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PLATE 4

Plate 5. Hybrids *Paecilozonites cupula* × *P. bermudensis* and coloration of *P. bermudensis*

Figures

1. Hybrids, *Poecilozonites cupula* × *P. bermudensis*. From locality 3, Harrington Formation. 1a, *cupula*-like coloration 12^{n}3. 1b, intermediate. 1c, *bermudensis*-like coloration 1(23). MCZ 29004. × 2.

2. Hybrids, *Poecilozonites cupula* × *P. bermudensis*. From locality 69, formation unknown. Intermediate in color and form. MCZ 29005. × 2.

3. *Poecilozonites bermudensis zonatus* Verrill. From locality 67, formation unknown. 12(3S) coloration. MCZ 29001. × 2.

4. *Poecilozonites bermudensis zonatus* Verrill. From locality 5, Shore Hills Formation. 123 coloration. MCZ 29002. × 2.

5. *Poecilozonites bermudensis zonatus* Verrill. From locality 36, Southampton Formation. Illustrated to show "faded" color variation in which bands of color are replaced by lines at the previous band peripheries. MCZ 29003. × 2.

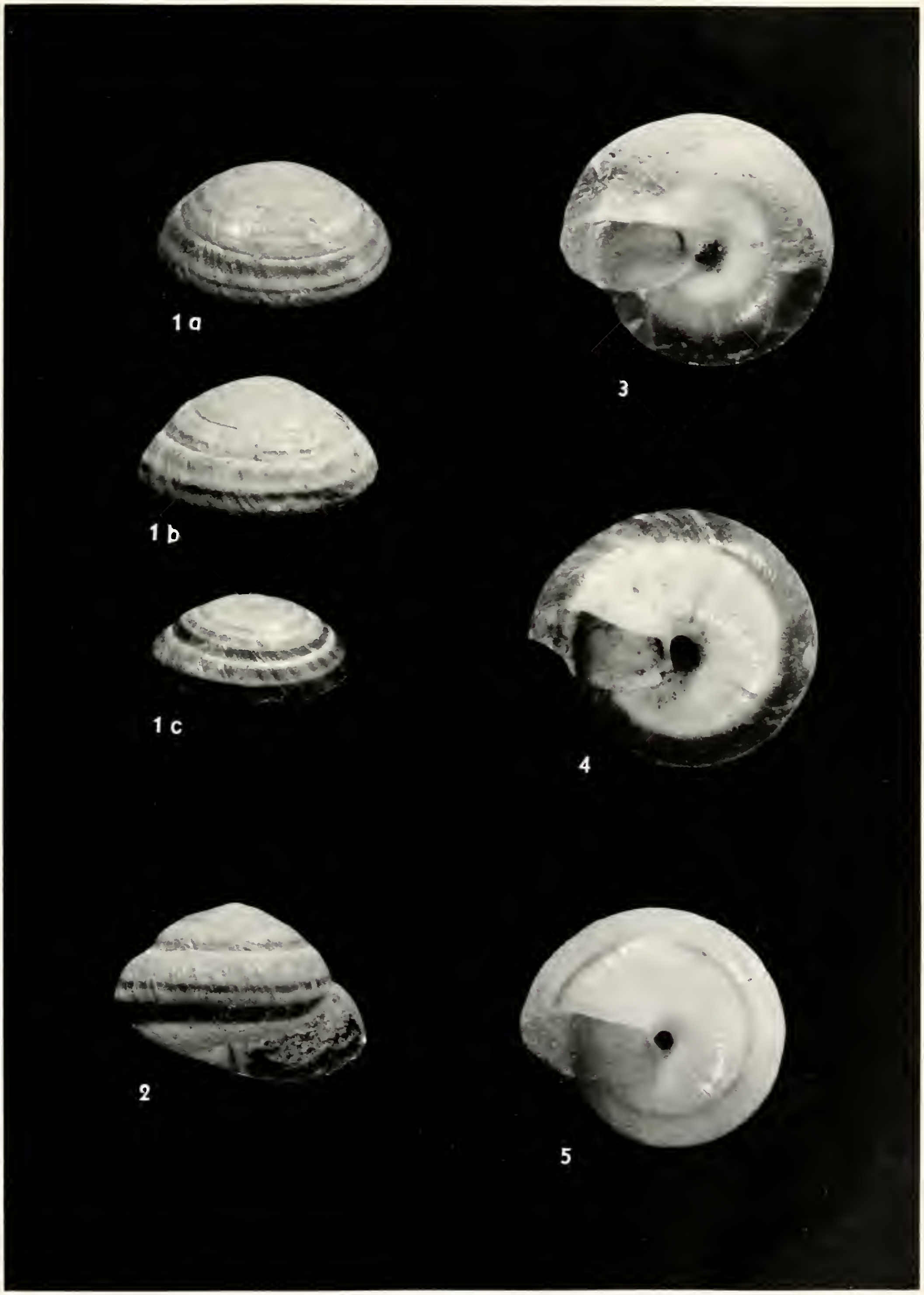

PLATE 5